ARBOREAL LIFE
AND THE
EVOLUTION OF THE HUMAN EYE

· F · TREACHER COLLINS ·

Head of an Adult Male Mandrill.

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AND THE

EVOLUTION OF THE HUMAN EYE

A REVISED PUBLICATION OF THE

BOWMAN LECTURE

DELIVERED BEFORE THE OPHTHALMOLOGICAL SOCIETY OF THE UNITED KINGDOM IN MAY, 1921

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PREFACE.

It is customary for the rising generation to regard the Victorian Era as characterized by the wearing of preposterous clothing, and by living in rooms full of ugly furniture, with decorations devoid of taste. However these things may have been, there can be no doubt that it was an era which produced a number of scientific men of outstanding ability, whose like we shall not look upon again.

One of these great Victorian scientists was Sir William Bowman, who, early in his career, earned for himself a world-wide reputation by the number and accuracy of his investigations into the minute anatomy of the various tissues of the body. Some of his most important observations were in connection with the minute anatomy of the eye; and though originally a general surgeon, so great a repute did he gain as an ophthalmologist that he was gradually forced to restrict his practice to that branch of his profession.

During the middle part of the Nineteenth Century, Bowman was the most prominent ophthalmologist in England, as von Graefe was in Germany and Donders in Holland. These three distinguished men came together for the first time at the Moorfields Hospital in the summer of 1851, the year of the Great International Exhibition in London. Linked together by the pursuit of knowledge in a branch of their profession, which was at that time growing in a most exciting fashion, they became the firmest of friends

for the remainder of their lives. In the year they first met, Helmholtz had invented the ophthalmoscope, whereby, as von Graefe said, a new world became opened up for exploration. In the same year Dr. A. Cramer, working under Donders' guidance, by observing alterations in curvature in the anterior surface of the lens, discovered the seat of accommodative power, while Bowman, but a few years previously, had demonstrated the muscular character of what had up to that time been regarded as the ciliary ligament.

So great was Donders' regard for Bowman that he dedicated his epoch-making book to him in the following glowing terms:

"To William Bowman, F.R.S., whose merits in the advancement of physiology and ophthalmology are equally recognized and honored in every country, this work on the *Anomalies of Refraction and Accommodation* is in testimony of the warmest friendship and of esteem inscribed by the author."

When, in 1880, the Ophthalmological Society of the United Kingdom was instituted, Bowman was naturally elected its first president. He held the post for three years and manifested the greatest interest in the society's progress and prosperity. In 1883, the council of the society passed the following resolution: "That in recognition of Mr. Bowman's distinguished scientific position in ophthalmology and other branches of medicine, and in commemoration of his valuable services to the Ophthalmological Society, of which he was the first president, the council shall each year, or periodically, nominate some person to deliver a lecture before the society, to be called The Bowman Lecture, which shall consist of a critical résumé of recent advances in ophthalmology or in such subject or subjects as the council shall select, or of any original investigation, and shall be delivered

at a special meeting of the society held for the purpose, at which no other business shall be transacted."

No better method could have been adopted for paying tribute to the character and attainments of Sir William Bowman than the institution of such a lectureship. Great as were his own original contributions to ophthalmology, he probably did still greater work for it by the stimulating and kindly help he rendered to others. It seems, therefore, most appropriate that his name should continue to be associated with original work, not only that of his own countrymen, but also that of distinguished ophthalmologists from other parts of the world.

The Bowman Lecture which is here reprinted from Vol. XLI of the *Transactions* of the Ophthalmological Society is the twenty-second that has been given. The names of those who have delivered the preceding twenty-one are as follows: Sir Jonathan Hutchinson, F.R.S.; J. Huglings Jackson, M.D., LL.D., F.R.S.; Prof. Zehender (Rostock); Henry Power; Sir Henry Swanzy; Prof. Hansen Grut (Copenhagen); Priestley Smith; R. Marcus Gunn; Prof. E. Fuchs (Vienna); Sir F. W. Mott, K.B.E., M.D., F.R.S.; Prof. Sattler (Leipzig); Edward Nettleship, F.R.S.; E. Landolt, M.D. (Paris); Sir George Berry, M.D., LL.D.; v. Morax, M.D. (Paris).

The writer of this lecture cannot claim to have been a pupil of Bowman's, only a pupil of several of his pupils. From their lips and example he has, however, learned to reverence the work of their master and to try and follow humbly in his footsteps.

In the *Transactions* the lecture appeared under the title of "Changes in the Visual Organs Correlated with the Adoption of Arboreal Life and the Assumption of the Erect Posture." In the reproduction of it in book form a shorter title

has been thought desirable. The author wishes to express his indebtedness to the council of the Ophthalmological Society for its permission to reproduce some of the illustrations, and to his friend Dr. William Campbell Posey, at whose instigation and with whose kindly aid the lecture has been reproduced in its present form. E. T. C.

LONDON, 1922

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INTRODUCTION.

The influence of the environment in the production of changes in the visual organs is a large and interesting subject—so large that it is only possible to attempt dealing with a comparatively small part of it in this lecture. The part most full of interest to this society must necessarily be that which concerns the higher mammals. A study of the morphology of their visual organs shows that there is a very close resemblance between those of man and monkeys, and some very wide differences between those of monkeys and the lower mammals. The chief cause of these marked changes is, I propose to show, to be found in the alteration in environment produced by the adoption of arboreal life.

Dr. Wood Jones[1] in 1915 delivered a lecture at the Royal College of Surgeons "On the Influence of the Arboreal Habit in the Evolution of the Reproductive System," and I cannot do better than quote here the following passage from his opening remarks:

"No doubt the assumption of the upright posture has done much in putting the finishing touches upon the evolution of the human stock, but we must be careful to give it no more than its real value. Long before the fashion of walking upright had been even foreshadowed in the crouching gait of the half-finished product, a potent factor was

at work producing those changes which ultimately permitted, and culminated in the erect carriage. This factor which paved the way, and to which most of the general changes of human and primate bodily conformation are due, was undoubtedly the arboreal habit, the habit of climbing and living up trees, instead of dwelling upon the ground beneath. We are too apt to lay too much stress upon man's descent from the branches. It was not coming down the tree that was so important in the evolution of the human stock; it was the climbing up, the first step toward the freedom of the branches, that counted in the progress of the mammalian stock from which man has sprung."

In this first lecture Dr. Wood Jones confined his observations to the evolution of the reproductive system, but at its close remarked "that every system and every part of man's body tell the same story." In three lectures delivered the following year he extended the subject, and dealt with the influence of the arboreal habit in the general evolution of man. It is my purpose in this lecture to discuss its influence in the evolution of the visual organs.

The life of mammals in their struggle for existence may be compared to a prolonged game of hide-and-seek. Some, like the Rodentia, have found safety by burrowing in the ground; some, like the Cetacea, by adopting aquatic life; some, like the Quadrumana, by climbing up into the trees; and others, like the Ungulata, by living in herds and acquiring protective coloration. The adoption of life in herds and protective coloration is a game at which two can play—the attackers and the attacked. Some of the Carnivora hunt in packs, and most of them have acquired colors and markings which serve as effective camouflage in the districts which they inhabit. For this great game of hide-and-seek the sense-organs have become developed to different degrees

in the various classes of mammals in accordance with their environments.

The herbivorous terrestrial mammals, whose safety and survival depend upon their swiftness of flight from danger, such as some of the Rodentia and the Ungulata, require sight, smell and hearing so developed as to enable them to detect quickly the approach of danger over a wide area. They grasp their food directly with their mouths, finding that which is suitable more by smell and by the touch of their acutely sensitive snouts than by sight. Their visual organs must, therefore, be adapted for the widest possible range of circumferential vision, sufficiently acute over a wide area to enable them rapidly to detect any moving object —such vision as is aptly termed "panoramic vision," the highest perfection of which may be described as vision which enables an animal to see in its entire circumference at one and the same time. They also require, to protect themselves from the evils which prowl by night as well as by day, a capacity for seeing in dim as well as in bright light.

The terrestrial carnivorous animals, with their powerful development of tooth and claw, require for their sustenance and survival smell and sight, which will enable them to track their prey and pounce accurately upon it when within a suitable distance. They grasp their food with their mouths, steadying it with their front paws while tearing it to pieces with their teeth. Their visual organs must, therefore, be so adapted that they can concentrate the sight of both eyes on their victims at the distance from which they spring, and follow quickly any movements such victims may make in their endeavors to escape. For these purposes binocular vision is more essential than panoramic vision. As the animals upon which these Carnivora prey are comparatively large, accurate vision for fine detail is not requisite. Good

vision in dim lights, rather superior to that of their victims, is essential for success in their pursuits.

Mammals like the Simiæ, who have found safety from carnivorous foes by life in the trees, have in learning to climb acquired the capacity of using their forelimbs for prehensile purposes. They require sight which will enable them to swing and spring with accuracy from bough to bough. Assuming the semierect posture, they grasp their food with their hands and convey it by them to their mouths. Their visual organs have, therefore, to be adapted for considerable accuracy in the judgment of distances, varying considerably in degree; hence not only binocular vision but stereoscopic vision is required, together with accurately associated powers of accommodation and convergence. As the food of these arboreal mammals consists of fruits and insects, which they pick up with their fingers, they require color-sense and a high degree of acuity of vision for small objects. Safe in their arboreal resorts, away from the dangers which prowl by night in the land below, vision in dim lights is not so essential for their safety as it is for some other classes of mammals.

Man, having descended from the trees and become a hunter and also exposed to the attacks of carnivorous foes, has succeeded in maintaining his existence by the assumption of the erect posture, which has entirely freed his forelimbs for the use of weapons of offence and defence. The manufacture and use of such weapons has necessitated increased precision in the judgment of distances and of concentration in the thoughtful recognition of detail. The elevation of his head, due to his erect posture, has increased his range of circumferential vision. Having acquired during arboreal life a more acute central form-sense than any other terrestrial mammal, together with the most highly-developed stereo-

scopic vision, he has, by extended and more rapid movements of both eyes and head, increased the range of his field of fixation.

The different visual requirements thus outlined for different forms of environments have involved considerable alterations in the structural architecture of the visual organs. It is with these structural alterations that I now proceed to deal, dividing them up for descriptive purposes under the following headings: I. The Field of Vision; II. Light-sense; III. Form-sense; IV. Accommodation and Convergence; V. Color-sense; VI. The Protective Mechanisms of the Eyeball.

CHAPTER I.

THE FIELD OF VISION.

In studying the modifications met with in the visual organs in the various species of Mammalia, to allow for different requirements in connection with the visual field, we have to take into consideration the monocular field, the combined monocular fields, the binocular field and the field of fixation.

The extent of the monocular field may be modified by the degree of prominence of the eye in the head, and by structural alterations in the eye itself.

In animals in whom a large monocular field is of the greatest importance, such as those who depend for safety on their rapidity of flight, the eyes are found set prominently out from the surface of the head. In the Ungulata the outer margin of the orbit is composed of a complete projecting bony ring which serves to hold the eyeball prominently forward (Fig. 1). In the Rodentia, the Insectivora and the Carnivora the orbital ring is incomplete externally, in the latter the malar and frontal apophysis being only united by fibrous bands (Fig. 2).

The evolution from an incomplete to a complete bony ring at the margin of the orbit can be well traced in the ancestry of the horse. In the *Meso-hippus baridi,* its three-toed ancestor, from the lower Miocene tertiary of North America, the bony wall of the orbit is open behind.

In monkeys, anthropoid apes and in man the bony

apophyses of the outer margin of the orbit are in contact, and it is shut off from the temporal fossa by the orbital plates of the malar and sphenoid bones, so that the orbit

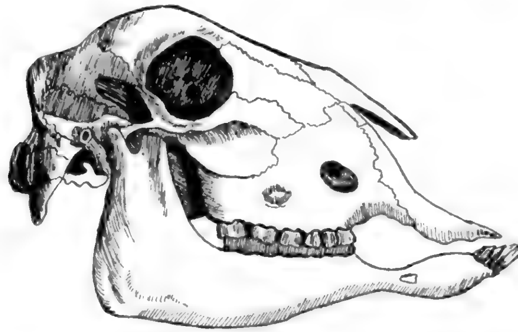

FIG. 1.—Skull of a hornless sheep. (After Owen.)

becomes a more complete bone-lined recess than in any other class of mammals. In some lemurs a similar separation of the orbit from the temporal fossa is met with, but in the majority of them no such complete separation has taken

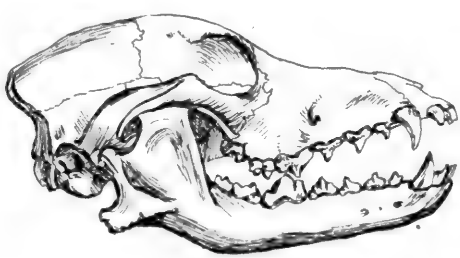

FIG. 2.—Skull of a dog.

place. The closing in of the outer wall of the orbit in Primates does not give prominence to the eye and enlarge the monocular field as in the Ungulata, but ensures steadiness

of the movements of the eye in the interests of binocular vision.

Some mammals have the power of markedly increasing the prominence of the eyes in the orbit, and so temporarily of increasing the extent of their monocular fields. In burrowing animals, such as moles and hedgehogs, the eyes are retracted, for the sake of protection, when they are below ground, and are protruded, beyond their epidermal coverings, when they come to the surface. In other mammals increased prominence of the eyes becomes most noticeable when they are alarmed, and when increased circumferential vision is most likely to be of importance to them. The increase in the prominence of the eyes is effected by relaxation of the retractor bulbi muscle, and contraction of the muscle of Gegenbauer, which lines the fibro-elastic tissue filling in the outer wall of the orbit in animals where it is not bounded by bone. A vestige of this muscle is sometimes to be found in man opposite the sphenomaxillary fissure, and is termed Müller's muscle. I shall have more to say respecting it later, in speaking of the protective mechanisms of the eyeball. I refer to it here because slight protrusion of the eyes in human beings, as the result of intense emotional excitement, has been observed; though "starting of the eyes from the head" as the result of fright is more often read of in fiction than actually seen in real life.

An increase in the size of the cornea relatively to the size of the eyeball must allow rays of light of greater obliquity to be refracted into the eye, and an increase of the corneal surface tends to increase not only the size of the field of vision, but also the clearness of peripheral images.

In some rodents the cornea composes nearly half the surface of the eyeball. The relations between the diameters

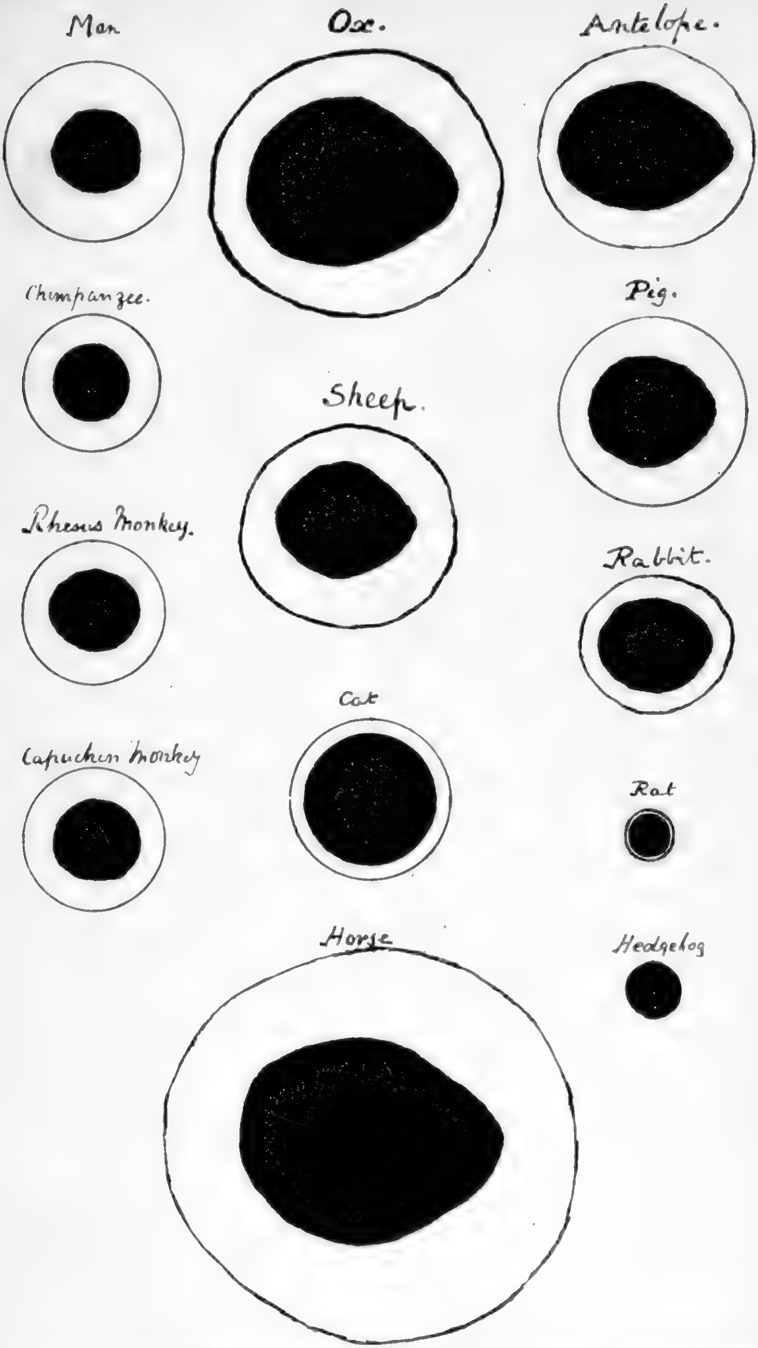

FIG. 3.—Showing size of cornea in relation to size of eyeball. Drawn to scale.

of the eyeball and the cornea of mammals are shown in the following table (Fig. 3.):

	Diameters of the eyeball.		Diameters of the cornea.	
	Antero-posterior.	Lateral.	Lateral.	Vertical.
Man	24.8 mm.	24.4 mm.	11.6 mm.	11.0 mm.
Chimpanzee	19.0 "	18.0 "	10.5 "	
Rhesus monkey	19.5 "	19.0 "	12.0 "	11.0 "
Capuchin monkey	18.5 "	19.0 "	11.0 "	10.5 "
Cat	22.0 "	21.0 "	18.0 "	
Horse	44.0 "	54.0 "	34.0 "	27.0 "
Ox	36.0 "	38.0 "	27.0 "	22.0 "
Sheep	27.0 "	28.0 "	19.0 "	15.5 "
Antelope	27.0 "	29.0 "	22.0 "	18.0 "
Pig	23.5 "	24.0 "	17.0 "	14.0 "
Wallaby	18.0 "	19.0 "	14.0 "	
Rabbit	16.0 "	20.0 "	15.0 "	
Rat	5.5 "	5.5 "	5.0 "	5.0 "
Hedgehog	6.0 "	6.0 "	6.0 "	6.0 "

In man and monkeys, where a central spot of distinct vision is of the greatest importance, the size of the cornea relatively to the size of the eyeball is comparatively small. Thus in all mammals below man the diameter of the cornea measures more than half the antero-posterior diameter of the globe. In the chimpanzee it is about half and in man considerably less than half.

Mammals that have a proportionally large cornea have also a proportionally large lens which is nearly spherical in shape, there being only a very slight increase in the size of the lateral diameter over that of the antero-posterior (*vide* table, p. 70). In man and monkeys, where the cornea is proportionally small, the lens is also proportionally small and considerably flattened from before backward. In monkeys the antero-posterior diameter of the lens is a little more than half the lateral diameter and in man about half.

Emmert[2] has estimated the relation of the size of the lens to the size of the eyeball as follows:

Horse	6 to 100
Ox	7 to 100
Calf	5.5 to 100
Sheep	7.6 to 100
Pig	8 to 100
Dog	7.7 to 100
Cat	10 to 100
Rabbit	8 to 100
Man	4.2 to 100

As pointed out by Lindsay Johnson,[3] with a large spherical lens, rays falling obliquely on the cornea will be brought to a focus with comparatively little distortion, the image being received upon a surface which is nearly equidistant from the nodal points. This is a matter of considerable importance in securing a large monocular field for moving objects, in animals with a retina having a widely-extended sensitive area. In the Primates, who require acute vision for small fixed objects, and who have developed a highly sensitive, small, central spot for this purpose, it is essential that the image of the object looked at should be accurately focussed on that spot only. It is advantageous, in the interests of binocular vision, that the images of objects formed on parts of the retina peripheral to the central spot should be but dimly seen. Hence we find in the Primates the cornea and lens so constructed as to sacrifice the interests of the monocular field in favor of those of acute central fixation.

The alteration in the shape of the lens in Primates, so that instead of being nearly spherical it is considerably flattened antero-posteriorly, has considerably diminished its refractive power. To compensate for this to some extent we find that the refractive power of the cornea has been considerably increased. The following interesting table has been constructed by Kalt and Dufour;[4] it shows that in the eyes of man and birds, which have flattened lenses, the refraction of the cornea relative to that of the lens is

considerably greater than it is in other mammals and in fishes, which have rounder lenses.

	Focal distance of the cornea.	Focal distance of the crystalline lens.	Relation: 1 to—
Man	31.2 mm.	49.2 mm.	1.60 mm.
Crow	25.8 "	36.7 "	1.42 "
Horse	78.8 "	64.4 "	0.82 "
Dog	33.8 "	22.9 "	0.60 "
Whale (out of water)	314.3 "	40.5 "	0.13 "
Carp	38.0 "	6.6 "	0.17 "

Most of the Ungulata have markedly oval corneæ, their lateral diameters measuring more than the vertical. In sheep there is a difference of 3.5 mm. between the two, and in the ox 5 mm. Associated with oval corneæ they have oval pupils elongated laterally. According to Eversbusch,[5] this is due to the presence of a check ligament, extending from the pupillary margin to the periphery, which can be seen as an elevation on the posterior surface of the iris. I have examined the iris of several different species of Ungulates, but have been unable to find any such check ligament. The elongation of the pupil can quite adequately be explained: First, by the elongation of the cornea, to which the root of the iris is attached laterally; and secondly, by the length of the iris in the vertical plane being greater than in the horizontal. In a horse's iris I find there is 2 mm. difference in the length of the iris horizontally and vertically (Fig. 4). There is also, in these animals with a horizontally oval pupil, a difference in the length of the ciliary body horizontally and vertically. In the horse the distance from the root of the iris to the ora serrata measures 5 mm. horizontally and 10 mm. vertically. To put it another way, the retina extends farther forward laterally than vertically in the Ungulata, which have pupils and corneæ elongated laterally. The combined effect of these three anatomical features is to pro-

duce an extension of the monocular field of vision in the horizontal plane.

In the center of these elongated oval pupils a deeply-pigmented elevation is met with at both the upper and lower borders, but considerably larger and more raised at the upper than the lower (Fig. 5). This elevation has received the name of the "corpus nigrum." In a horse,

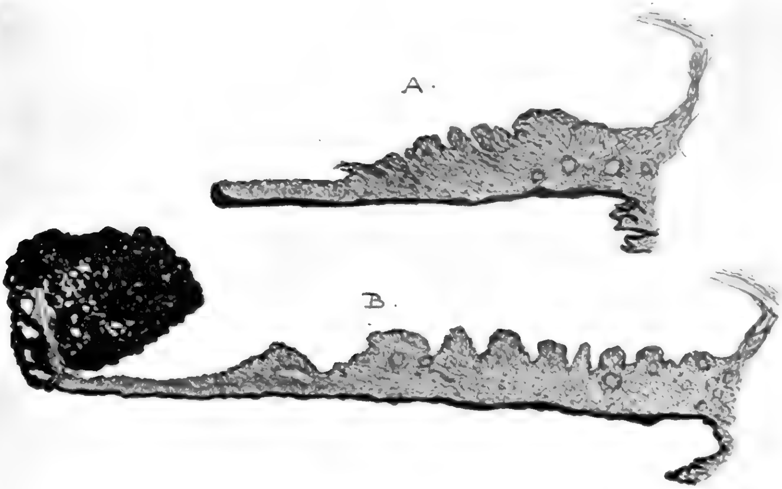

Fig. 4.—Sections through the iris of a horse. *A*, in the horizontal meridian. *B*, in the vertical meridian.

the lateral diameter of whose pupil measured 17 mm., the corpus nigrum at its upper border measured 8 mm. in length, 3 mm. in width and 3.5 mm. in height. In sections of the iris it can be seen to be an extension forward from the pigment epithelium on its posterior surface, *i. e.*, a growth forward from the anterior extremity of the secondary optic vesicle (Fig. 4 *B*). It is a vascularized structure and so has some elements of mesoblastic tissue in it. Bleached

sections show the mass to be made up of flattened epithelial cells, which line and form columns between numerous, variously-sized circular spaces.

The function of the corpus nigrum has so far not been definitely determined. Lindsay Johnson[3] suggested that it served as a shade for the large oval pupil. Such a suggestion does not explain the presence of a projection from the lower margin of the pupil as well as the upper. In some animals,

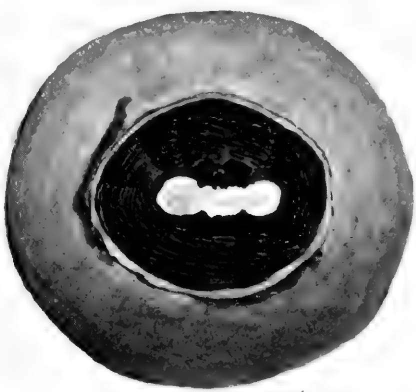

FIG. 5.—Front of horse's eye from which cornea has been removed to expose iris with the "corpus nigrum."

e. g., gazelles, camels and llamas, the black bodies from the upper and lower margins of the pupil have indentations capable of fitting into one another. On examination of horses' eyes, when exposed to bright sunlight, I have observed that contraction of the pupil causes the pigmented bodies from the two borders to meet and fill up its center, leaving the two extremities still open. So that the horse then has, instead of one oval pupil, two circular ones, looking

respectively forward and backward. A large oval pupil, while affording a wide range of lateral vision, must detract very considerably from the clearness of vision by not having the stenopaic effect of a round pupil. I would suggest that one function of the corpus nigrum is at times to compensate for this defect by the conversion of the oval pupil into two round ones.

Animals, such as the terrestrial herbivorous mammals, who require panoramic vision, have their eyes set laterally in the head so as to obtain the largest circumferential effect of the combined monocular fields. Lindsay Johnson[3] measured the divergence of the optical axes in a large number of representative animals, and constructed a diagram graphically showing how it varies in the different natural orders, families, genera and species. From this it is seen that the most laterally placed eyes are met with among the Rodentia, the Marsupialia and the Ungulata. The greatest divergence is in hares, whose optical axis in each eye measures 85° of divergence from the middle line. It seems probable that they, and some of the other rodents, have complete panoramic vision, *i. e.*, are able to see in their circumference at one and the same time.

Among the Carnivora the smallest amount of divergence is in lions and cats, in which it is less than 10° in each eye. The Simiæ and man alone among mammals have parallel optic axes.

This movement forward of the optical axes toward parallelism is clearly in the interests of binocular vision, and at the sacrifice of the range of simultaneous circumferential vision. As ontogeny is a condensed recapitulation of phylogeny, it is interesting to note that in the human embryo the optic vesicles when first formed are directly opposite to one another, from which position they gradually turn

forward, so that at the third month of fetal life the optic axes of each eye diverge 45° from the middle line; before birth they become parallel.

Wood Jones[1] has described how the alteration in the position of the eyes in mammals is due to the recession of the snout. He says: "When an animal has a fully elongated snout region, it may be said to possess a long face with an eye situated upon each side of it; but when the snout region has undergone complete recession, it may be said to have a flat face with two eyes situated upon the front of it. The mere fact of the recession of the snout produces this change, for the two eyes are turned to the front as the elongated muzzle shrinks between them."

He further points out this recession of the snout is the result of (*a*) the substitution of the hands for it as the chief means of tactile exploration; (*b*) the decrease in the use of the jaws for seizing and tearing food; (*c*) the diminished importance of the sense of smell.

The three changes are all the outcome of the adoption of arboreal life. It has resulted in the use of the forelimbs for grasping purposes. From this they have gradually acquired acute tactile sensibility, and have superseded the snout as a means for exploration by the sense of touch; the latter has, therefore, tended to atrophy from disuse. From the grasping of boughs in arboreal life has arisen the power of grasping food with the hands to convey it to the mouth instead of seizing it primarily with the jaws. This diminished use of the jaws has led to their loss of prominence and power. "No trail of scent is laid among the branches of a tree" (Wood Jones). "Life amid the branches limits the usefulness of the olfactory organs" (Elliot Smith).

Binocular vision is produced by the overlapping of the fields of vision in the two eyes. In Cetaceans so massive

is the head, and so far back are the eyes set, that it is impossible for any such overlapping to occur (Fig. 6). In rodents, such as rabbits and hares, which also have their eyes set far back, the overlapping of the fields anteriorly cannot exceed more than 15°.

It has been suggested by Grossman and Meyerhausen[6] that in these animals some overlapping of the fields may occur posteriorly, and that in them a certain amount of posterior binocular vision may be present. As all sportsmen know, rabbits and hares see very imperfectly when danger is immediately in front of them, and will run straight forward

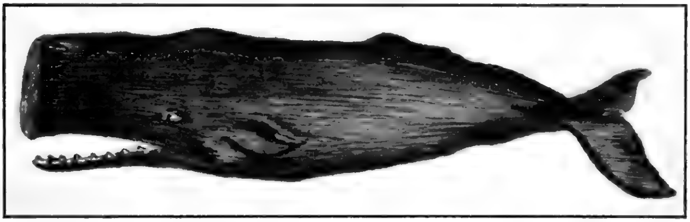

Fig. 6.—Sperm whale.

toward a gun. I am told that it is a general belief in the country, that if a hare lies in a furrow with the nose pointing down it, you can walk up the furrow to the hare's head.

In connection with the binocular vision of mammals it is important to note the observations of Kalt[7] as to the size of the angle γ in the different species. He states that "in the human species the visual axis pierces the cornea 5° inside its center. In the higher monkeys it is almost the same, but one sees this angle increase as one descends the animal scale. It is 15° in the Lemuridæ, 20° to 26° in the Carnivora, and it varies between 55° to 63° in the Herbivora." The increase of the angle tends to balance to some extent

an increase in divergence of the optic axes, so that animals with a wide divergence are still able to see binocularly.

A horse with eyes set prominently forward, large corneæ and laterally oval pupils, can see behind and observe the out-kick of its hind leg without turning its head. With a visual axis piercing the cornea 50° to 63° inside its center, with the corpus nigrum capable of closing in the middle part of the oval pupil and leaving a circular one looking forward, and with about one-sixth of the fibers of the optic nerve turning into the optic tract of the same side while the rest decussate, a horse evidently possesses binocular stereoscopic vision, which must be of the greatest assistance to it in the estimation of size and distance in jumping. Every horseman knows that an object at which a horse is most likely to shy is one situated at the side and of a light color. To prevent shying we put blinkers on harness horses, so that they may not see these laterally placed objects, but only those which they view binocularly straight in front of them. In training a shying horse it is customary to walk the animal up to any object it has shied at with its head toward the object, which it can then view binocularly.

Closely associated with the varying degrees of binocular vision we meet with varying degrees of decussation of the fibers of the optic nerve at the chiasma. This matter has been dealt with very fully by Dr. Wilfred Harris.[8] He considers that binocular vision is associated with carnivorous habits; it is met with in carnivorous fishes, amphibia and birds. In all these there is total decussation of the optic nerve fibers at the chiasma, so that they do not have stereoscopic vision as in mammals, in many of whom, owing to semi-decussation of the fibers at the chiasma, visual impressions from the two eyes are received on the same side of the brain.

Rodents have no conjugate movements of the eyes, and no consensual response of the pupils to light, only a direct reaction. Singer and Münzer[9] found that in mice and rats the decussation of optic nerve fibers at the chiasma was complete. Wilfred Harris examined the optic nerves, chiasma and tracts of rabbits in sections stained with hematoxylin by Pal's method, and also a fortnight after the experimental enucleation of one eye, by staining with Marchi's method, to trace the degenerated fibers. He found that decussation was almost complete, only very few fibers, here and there, turning round from the optic nerve into the optic tract of the same side. Ramon y Cajal[10] obtained similar results.

In the Ungulata it is difficult to observe the movements of the two eyes at the same time, but it appears that they are to some extent conjugate. In them the decussation of the optic nerve fibers at the commissure is not complete. In the horse and calf, two observers in Vienna, using Marchi's method, found that about one-sixth of the fibers turn into the optic tract of the same side.

In the carnivorous mammals there is consensual reaction of the pupils to light, and the movements of the two eyes are more obviously conjugate than in the Ungulata. Wilfred Harris found that experimental division of the optic tract on one side in cats produced distinct homonymous hemianopsia, with the hemianopic pupil reaction to direct light in the opposite eye, though its consensual reaction was brisk on exposure of the other eye to light. Microscopically he found, in sections of the chiasma of a cat stained with Marchi's method, after enucleation of one eye a fortnight previously, that a large proportion of degenerate fibers were present in the optic tract of the same side. These degenerate fibers were spread equally through all parts of the tract and not collected into any distinct bundle.

In monkeys and in man there are conjugate movements of the eyes, and consensual reaction of the pupils to light, as in the Carnivora, but in addition they have a very highly developed spot of central vision with a special bundle of nerve fibers leading from it, and highly developed powers of convergence and accommodation.

There is no very definite anatomical evidence as to the course taken by the macular nerve fibers at the chiasma. Cajal[10] discovered bifurcating fibers in the chiasma of the rabbit, the divisions passing into the two optic tracts. Kölliker[11] found similar bifurcations in the chiasma of a cat a few days old. It was upon these observations that Wilbrand based his hypothesis as to the escape of the macula in cases of bilateral hemianopsia.

He attributed it to the bifurcation of fibers coming from each macula at the chiasma, so that both maculæ were connected with the occipital cortex on each side. There is, however, no evidence as to where the dichotomous fibers found in embryo cats come from, and in rabbits' retinæ no specialized central area, such as a macula, can be differentiated.

Usher and Dean[12] traced the course of degenerated nerve fibers in the optic nerve and chiasma in monkeys after experimental lesions in the retina at the macular region. In summing up their results they say: "As regards the question whether the macular fibers cross wholly or partially in the chiasma, it is impossible from our experimental cases to make a definite statement, owing to the difficulty that exists in determining whether the wound was limited to the macular fibers or, on the other hand, whether it had damaged only a portion of these; while in Case 11 the decussation was complete, in Case 10 there were uncrossed fibers, even at the most posterior part of the chiasma."

Though the anatomical evidence as to the course taken by the macular fibers in the chiasma is very uncertain, it seems highly probable, on physiological and clinical grounds, that semi-decussation of them takes place. It would be

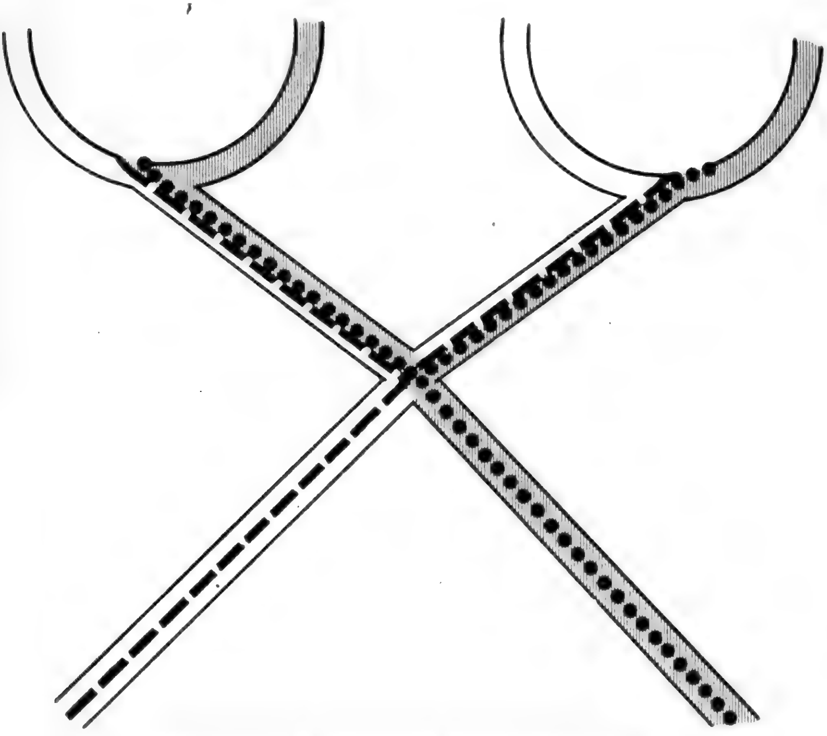

Fig. 7.—Diagram to show hypothetical semi-decussation of macular nerve fibers at the chiasma.

difficult to understand how stereoscopic vision for detail could be brought about, unless the images coming from objects focussed on each macula were superimposed in the visual cortex. It seems most probable that in man and monkeys, not only are the visual impressions received from

the left halves of the two retinæ superimposed on the left half on the occipital cortex, and those from the right halves of the two retinæ on the right half of the occipital cortex, but that the impressions received from each macula are similarly superimposed on each half of the brain (Fig. 7). Clinically this view helps us not only in explaining the "macula escape" in cases of bilateral hemianopsia, but also affords an explanation of cases of central hemianopic defects without any peripheral contraction of the fields, an affection which, if right-sided, has the characteristic symptom of the patient finding a difficulty in reading while still retaining good central acuity of vision.

This semi-decussation of the nerve fibers from each macula is also, I suggest, of interest in connection with the causation of certain cases of congenital concomitant strabismus. As we all know, there are cases in which children have perfect acuity of vision in each eye, with little or no refractive error, who never at any time make an attempt to use the two eyes together, nor can they by any means be induced to do so. A very simple explanation of such cases might be found in a congenital defect in the course of the macular nerve fibers, whereby complete decussation, instead of semi-decussation, had taken place. With complete decussation the impression received by the visual cortex from each macula would be unilateral instead of bilateral, as with semi-decussation. The acuteness of perception would not be affected by the complete decussation, only the stereoscopic effect. The anatomical evidence in proof of this hypothesis would be exceedingly difficult to obtain. Clinical evidence might, however, be forthcoming should a patient having such a congenital concomitant strabismus subsequently develop a homonymous bilateral hemianopsia, in which case, if this hypothesis be true, we should expect to find the

whole macular region on one side included in the blind area.

Conjugate movements of the eyes in the vertical plane are innate in the human infant, but in the horizontal plane are only gradually acquired during the first six months of life.

From the early development of conjugate movements in the vertical plane we may infer that man's mammalian forbears were exposed to dangers which attacked them from overhead, in the way in which small rodents are now attacked by carnivorous birds. The development of conjugate movements in the lateral plane followed later, with the shrinkage of the snout and the translation of the eyes forward in the head.

The development of acute, central, stereoscopic vision for form, together with corresponding points in the two retinæ, introduces a fresh factor in connection with the field of vision—that is, the field of fixation. Though no mammals below monkeys have a capacity for distinguishing detail, such as is associated with the presence of a fovea centralis, there is evidence to show that in some, especially the Carnivora, there is an area centralis in the retina more acutely sensitive to form than the periphery. Such animals can fix an object and make movements of the eyes to maintain fixation, *e. g.*, when a cat follows the movements of a mouse. The field of fixation becomes, however, of greater importance with the increased acuity of central stereoscopic vision, such as has been developed in association with arboreal life. Still more is it important to man, who has assumed a fully erect posture and become exposed to the dangers of terrestrial life by his descent from the trees. The rapid movement of the highly-developed spots with acute form-sense, from one object to another in his circumference,

more than compensates man for the loss of the wide degree of panoramic vision which the alteration of position of the eyes from the side to the front of the head entails. For these rapid changes of position of the spots with acute form-sense, increased mobility, first, of the eyeballs, and secondly, of the head, has been evolved.

Though nearly all mammals have, as in man, four recti and two oblique muscles connected with the eyeballs, the movements of the globes in all those below monkeys are comparatively slight. It is in association with the development of acute central stereoscopic vision, as in monkeys, that the movements of the eyes become a conspicuous feature. The range of such movements becomes considerably extended in man, and may, I suggest, be correlated with the full assumption of the erect posture and the greater need for a wide, quick circumferential vision on the ground than in the trees.

It is probably for the purpose of increasing the range of movement of the eyes that man has developed a wider palpebral fissure, in proportion to the width of the cornea, than is met with in any other mammal. The effect of this proportional difference is that a large part of the ocular conjunctiva, with the sclerotic beneath, becomes exposed to view. In no other mammal are "the whites of the eyes" such a conspicuous feature as in man. An exposure of the ocular conjunctiva in this way has rendered it liable to irritation from atmospheric influences, more especially on the inner side of the globe, where, due to the presence of the lacrimal bay, the largest area is uncovered, and where, in mammals other than Primates, a special protection is afforded by the membrana nictitans. Irritation of this sort from atmospheric influences, when excessive, gives rise to the diseased conditions known as "pingueculæ" and

"pterygium"—affections which are not met with in other mammals than man.

Wood Jones[1] has described how the changed relations between the long axis of the skull and face and the long axis of the vertebral column, which is produced in monkeys as the result of arboreal life from the partial assumption of the upright posture, has resulted in a changed position of the occipital condyles on the base of the skull, which hinge it to the vertebral column. In quadrupeds these condyles are situated at the posterior extremity of the skull. In most monkeys they are situated well forward on the base; in anthropoids still farther forward; in man, who has assumed the permanently erect posture, the head is practically balanced upon the first cervical vertebra.

As the head becomes more nearly balanced on the vertebral column, so the powerful ligamentous and muscular attachments which pass between its posterior surface and the cervical spinous processes become reduced in strength, and the spinous processes themselves become reduced in size. The even balancing of the head on the spine, and the reduction in size of the cervical spinous processes, both tend to facilitate the range and rapidity of the lateral and rotatory movements of the head. Such increased movements of the head, like the increased movements of the eyes, serve to increase the area of the fields of fixation.

CHAPTER II.

LIGHT-SENSE.

THE most primitive visual function is the perception of light, and the eyes of some animals are so constructed that this would seem to be the only purpose for which they exist.

According to Prof. Elliot Smith,[1] in the forerunners of the Mammalia, and in the primitive mammals themselves, the senses of sight and hearing were but poorly developed compared with that of smell. "This was due," he says, "not only to the fact that the sense of smell had already installed its instruments in, and taken possession of, the cerebral hemisphere, long before the advent in this dominant part of the brain of any adequate representation of the other senses, but also, and chiefly, because to a small land-grubbing animal the guidance of smell impressions, whether in search for food or as a means of recognition of friends or enemies, was much more serviceable than all other senses. Thus the small creature's mental life was lived essentially in the atmosphere of odors, and every object in the outside world was judged primarily and predominantly by its smell, the sense of touch, vision and hearing being merely auxiliary to the compelling influence of smell."

The smallest and least developed eyes in existing mammals are found in moles, hedgehogs, insectivorous bats and cave-rats. All of them are nocturnal in their habits and have only rods in their retinæ—no cones. The visual

function in these animals may be attributed entirely to the chemical reaction produced by light on the visual purple, which, through stimulation of the rods, starts a nervous impulse. These animals have a dread of light, or photophobia; when it appears the moles and hedgehogs at once return to their burrows, the rats retreat to the inner recesses of their caves, and the bats into the darkness of the foliage.

The photo-chemical reaction of the visual purple, besides providing for perception of light, could easily be amplified to provide for adaptation for different degrees of light, by the extent of the chemical reaction induced varying in accordance with the intensity of the illumination.

Trendelenburg[13] showed that there is a very close correspondence between the curve of scotopic luminosity in the human eye and that obtained from the bleaching of the visual purple of a frog's eye.

The time which it takes for the visual purple to reform in the rabbit's retina, after it has been bleached, coincides very closely with that which it takes the human eye to regain the approximately full power of dark adaptation after good light adaptation.

A bleached, undamaged, detached retina will remain bleached, unless brought back into contact with the pigment epithelium, when it will regain its violet color. From this, and from their anatomical arrangement, we may assume that the pigment epithelial cells are concerned in the manufacture of the visual purple. They are arranged like the cells in other secreting structures on a basement membrane, immediately beneath which is a rich vascular plexus, the capillary layer of the choroid. The fanciful suggestion made by Edridge Green,[14] that the visual purple is secreted by the rods, has nothing to support it, either anatomically or morphologically. The rods, from their

structure and connections, are obviously not secreting cells, but nerve end-organs.

Numerous careful and accurate observers have recorded how the visual purple is only to be found in the outer limbs of the rods and not in the cones. I have myself been able to confirm its absence from the cones in the retinæ of frogs and birds.

If, then, the rods react to the stimulus of light through the photo-chemical reaction of the visual purple, some other explanation has to be found for the reaction of the cones. A perception of light dependent entirely on changes in the visual purple would become abolished when it was bleached in bright light, and an animal with only rods in its retina would be blind under such circumstances.

The theory suggested independently by Max Schultze,[15] Parinaud and v. Kries,[16] which assigns different functions to the rods and cones, the so-called duplicity theory of vision, helps to explain so many of the visual phenomena met with in the human eye, both in health and disease, that it may well be accepted as a working hypothesis for the explanation of vision in other Vertebrata.

According to this theory the rods come into action in low degrees of illumination. They can only distinguish different degrees of light, not form or colors. The cones, on the other hand, come into action in high degrees of illumination, are capable of distinguishing the spectral colors, and of perceiving clearly the details of form. As Parsons[17] very aptly says: "Broadly speaking, vision with the dark-adapted eye, *i. e.*, scotopic vision, is monochromatic or tone-free. Vision with the light-adapted eye, *i. e.*, photopic vision, is polychromatic or toned. In the former the threshold stimulus intensity is low; in the latter relatively high."

Prisoners who have been confined in dark dungeons for a

long time, the congenitally total color blind, the mammals, already referred to, who have only rods in their retinæ, and nocturnal birds, all have a dread of light—that is, photophobia. They are all temporarily or permanently dependent for vision on perceptions received through their rods and the visual purple.

Those who have been exposed for a long time to glare, like sailors becalmed on a tropical sea, those who have the congenital affection which we call "night-blindness," or the acquired affection which is spoken of as "retinitis pigmentosa," and diurnal birds, all have a dread of darkness; that is a condition which I suggest may be conveniently termed "scotophobia." They are all temporarily or permanently dependent for vision on perceptions received through their cones.

No other photo-chemical substance has been discovered in the retina besides the visual purple. It becomes, therefore, natural to inquire whether some reaction other than chemical is not produced in the cones capable of originating a nerve impulse on stimulation by light.

Stort and Englemann[18] have described how a shortening of the inner segment of the cones takes place by the action of light and an elongation in darkness. On exposure to light, therefore, the outer segments of the cones are drawn toward the outer limiting membrane and away from the pigment-cells, while in darkness the opposite movement takes place. This effect has been observed in the retina of all animals hitherto examined, viz., fish, amphibians, reptiles, birds and mammals, including man. The part which moves actively is that which in its optical and chemical properties is like protoplasm, viz., the part of the cone between the ellipsoid and the cone nucleus, and to this they give the name of "cone-myoid." This movement in the cones may

be compared with the phototropic reactions met with in plant life, in hydra and in some small worms.

It would be a simple way of explaining the difference in the mode of stimulation of the rods and cones by light to regard that of the former as a photo-chemical reaction, and that of the latter as a phototropic reaction. Such an explanation would serve not only to account for the differences observed between rod and cone vision as regards light-sense, but also as regards form-sense, as I shall attempt to show in the consideration of that part of my subject. It is true that the contraction which has been observed in the cones resulted from a strong stimulus of some duration, but so far it is the only change of which we have any evidence as occurring in the cones apart from the rods; it is well, therefore, to see how far such a change will help in explaining visual phenomena.

The degree of illumination required to excite a phototropic reaction would be greater than that required to produce a photo-chemical reaction, so that we should expect rod vision, if it acted by the latter, to come into action with lower degrees of illumination than cone vision, if it acted by the former. Rod vision would fail in high degrees of illumination, due to complete bleaching of the visual purple; while cone vision, being capable of some degree of adaptation due to a varying degree of contraction of the cone-myoid in response to the amount of stimulating light, might continue active after the retina has been completely bleached.

As already mentioned, the mammals with the smallest eyes, who only expose themselves to very low degrees of illumination, have only rods in their retinæ. Those mammals who, though mainly nocturnal in their habits, enter rather more boldly into the light of day, such as rats, mice and rabbits, are found to have a few cones. Indeed, the amount

of daylight an animal exposes itself to and the number of cones met with in its retina correspond fairly accurately. The Simiæ, who, to obtain their food in their arboreal resorts (consisting, as it often does, of minute objects), require a high degree of illumination, have an area of the retina in which only cones are present, and in which they are closely congregated together. It would seem probable that it is due to this congregation of the cones together at the macula that man and monkeys can stand exposure to brighter daylight than any other mammal. Man's eyes cannot, however, stand exposure without damage to the same degree of

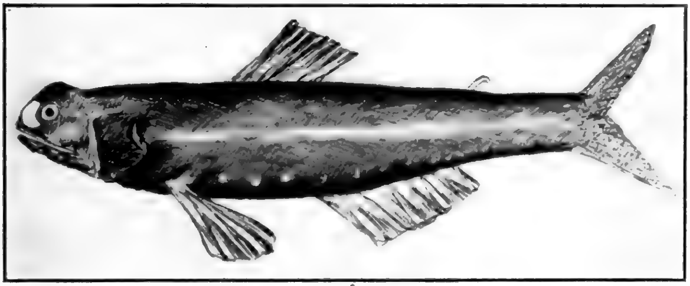

Fig. 8.—Headlight fish. Æthoprora lucida.

direct sunlight as some birds; eagles, for example, as they rise to fly will gaze directly at the sun without flinching. In the diurnal rapacious birds the retina has been found to be richer in cones than any other birds, or than any mammals.

Various means, supplementary to those in the retina itself, have been acquired by mammals to fit them for an environment having low degrees of luminosity. Some deep-sea fishes and cave-animals, who live in absolute darkness, have no visual sense and no visual organs, their survival depending on the acuity of their other senses. Other deep-sea fishes have evolved their own illuminating appliances, and

carry in front of them an apparatus capable of emitting a phosphorescent light (Fig. 8). In the eyes of pelagic fishes reflecting membranes are met with; on the surface of the iris is the membrana argentina, which gives it great brilliancy, and acts by reflecting light on objects looked at in dark places, much in the same way as that in which we employ our ophthalmoscopic mirrors. On the inner surface of the choroid they have another reflecting membrane, the tapetum lucidum, which intensifies the power of seeing in dim lights by reflecting rays back on the retina. The same device is met with in several classes of mammals; in the carnivorous Cetaceæ the reflecting membrane, as in fishes, covers the whole fundus; in the terrestrial mammals, where a tapetum is found, it covers only a sector of the fundus external to the optic disk. In the terrestrial Carnivora the tapetum is most brilliant and is composed of cells arranged in elongated plates together with hexagonal crystals. In the Ungulata the tapetum has an entirely different structure, being composed of layers of fibrous tissue and not cells. Among Primates a tapetum is met with in some lemurs with nocturnal habits, and is similar in construction to that of the Carnivora. Man and monkeys have no supplementary arrangement for seeing in dim lights such as that afforded by a tapetum lucidum. Monkeys, having resorted to arboreal life, where they found their food by day, and where they were safe from the attacks of carnivorous foes by night, have not had to acquire nocturnal habits. Man, having inherited his visual capacities from his arboreal ancestors, found himself, on his descent from the trees, more than equal to his mammalian foes by day, but inferior, and sadly handicapped, by night. Not only had he not acquired the advantages of a tapetum, but from prolonged life in the branches and reduction of the snout he had lost much of the protection afforded by acuteness of smell.

All children instinctively dread darkness and many persons can never free themselves from such dread throughout their lives. O. G. S. Crawford, writing in a recent number of the *Cornhill Magazine* on "Prehistoric Instincts," says: "Primitive man is an animal that lives and works by day. His habits are not nocturnal, and he seldom by choice goes forth from his lair during the hours of darkness. This love of daylight, and the corresponding aversion to darkness, is probably due to the great reliance he places upon sight; but, of course, the order of causation may have been reversed. We do not, however, find it in dogs, which rely on ear and nose. However this may be, there can be no doubt about the existence of an instinctive dislike of darkness in all of us today. This dislike is the pale survivor of a very real and acute instinct of fear innate in us, which dominates our childhood with all the vigor of its original force."

Primitive man, a mighty hunter by day, through the absence of a tapetum became a coward by night. A somewhat parallel instance may be referred to occurring among birds. They have no tapetum lucidum in their choroids, but in the retinæ of nocturnal birds rods are found to predominate very largely over the cones, while in the retinæ of diurnal birds the reverse condition is met with, the cones in them being far more numerous than the rods. The small diurnal birds, sparrows, chaffinches, redbreasts and such like, as soon as dusk begins to approach, seek concealment in bushes and hedges, where they will be safe from the dreaded attacks of the night owl. Should the owl prolong his hunting expeditions to such a distance that daylight overtakes him before he can return to his usual retreat, he becomes dazzled, is unable to proceed, and has to remain where he is until darkness again ensues. If during the daylight he

becomes discovered by the small diurnal birds upon which he usually preys, they at once recognize his plight and give him no mercy, mobbing him and pecking him with impunity. Thus through the specialized character of the end-organs of the retina the mighty hunter of the night becomes the abject victim of the day.

Primitive man, having abandoned the safety of the trees, sought protection from the perils that prowl by night in the natural recesses of the cliffs, and became a cave-living animal. Gradually he progressed to the hollowing out of caves for himself, and thus acquired the first step which led to the building habit. From this may we not trace the construction of lake dwellings, which by their situation afforded admirable protection from carnivorous foes, and later the more substantial houses of brick and stone, ultimately leading to all the glories of architecture?

It is probable also that fire, when first discovered by primitive man through hacking iron pyrites with a flint among dead leaves (Lubbock), was more valued for its illuminating than its heating properties. By the illumination which it afforded him at night his range of vision would become extended, and his struggle for existence against carnivorous mammals considerably assisted. From this first use of fire as an illuminant we can trace man's gradually increasing means of overcoming the dangers of darkness, until we arrive at the powerful searchlight of today which he employs both for purposes of attack and defence.

CHAPTER III.

FORM-SENSE.

Acuity of form-sense reaches its highest development among mammals in the Primates. Mammals as a class are characterized by the absence of a fovea, the Primates being the only ones in which it is to be found. In many mammals which do not possess a fovea there is an area centralis which approaches in structure the yellow spot; this can be recognized ophthalmoscopically, when the retinal bloodvessels are present, by the absence of them in that region and by their distribution around it. In sections this area centralis is distinguishable by an increased thickness of the retina, and microscopically by the arrangement of the cells. The increased thickness is due to the greater length of the rods and cones, their close congregation together, and the larger number of cells in the nuclear and ganglion cell layers associated with them.

Chievitz[19] and Slonaker[20] have examined the eyes of a number of different species of mammals anatomically, and the latter has published their combined findings in tabular form. In some animals, such as rats and bats, no central area is discoverable. In rabbits, most of the Ungulates and the fox, there is a horizontal bandlike area, which in the horse measures 5 to 7 mm. in breadth. Cats and some other Carnivora have a rounded central area. Krause[21] stated that cats possessed a fovea, but this was not found to be the case by Ganser[22] and Chievitz.[19] Lindsay Johnson[3]

sums up the correlation between the area centralis, the position of the eyes in the head and the shape of the cornea and lens as follows: "Sensitive areas of restricted dimensions, omitting those cases in which the area is limited to a macula, exist in the Carnivora, in which order the divergence is not great. In the Ungulates, Rodents, Edentates and Marsupials, where we find great divergence of the axes, large corneæ and nearly spherical lenses, the sensitive areas are larger, and probably the degree of difference in perception over such areas compared with the more peripheral parts is but little."

Among Primates a fovea is met with in man, anthropoid apes and monkeys, but not in lemurs. In Tarsius, which it is generally agreed is more nearly allied to Primates than it is to lemurs, Elliot Smith says, "There is no macula lutea." It is found in some reptiles, and is present in practically all birds. In writing of these latter, Casey Wood[23] says: "The depth of the fovea may be regarded as a measure of the sharpness of vision. Slonaker classifies foveæ as deep, medium and shallow. The round fovea is especially 'deep' in swift fliers and birds of prey; 'medium' to 'weak' in most birds, except that it is 'shallow' in the domestic pigeon and probably lacking in the hen."

Anatomically the fovea consists in man of an area measuring about 0.3 mm. in diameter, subtending an angle of about 70′, and lying almost exactly in the optic axis of the refractive media of the eye, at a point where the image projected by them is brought to the sharpest focus. It is characterized by an unfolding of the inner layers of the retina, which are spread apart so as to permit the direct unimpeded access of rays of light to the percipient end-organs of the retina. These end-organs consist exclusively of cones, and in the very center of the fovea (Dimmers' foveola) of cones

of a specially slender variety. Ramon y Cajal showed that each of the central cones is connected with but one bipolar cell and but one ganglion cell, thus differing from the end-organs in the more peripheral parts of the retina, each of which is connected with several bipolar and several ganglion cells.

The acuity of form-sense in man is most intense at the fovea and rapidly decreases on proceeding from it toward the periphery; thus it has been approximately estimated that 5° eccentric from the center of the fovea the acuity is reduced to $\frac{1}{4}$ and 20° eccentric to $\frac{1}{40}$.

In the development of the human retina an area centralis is recognizable before the fovea centralis makes its appearance. According to von Hippel,[24] in the central area of the retina at birth all the layers are recognizable, though in the situation where the fovea ultimately forms, the cells of the ganglion cell-layer and of the inner nuclear layer are somewhat thin and spaced out. By the end of the fourth week a depression is formed, but the full development of the fovea is not completed until several months have elapsed. This gradual unfolding of the fovea corresponds with what has been observed regarding the development of an infant's power of fixation. Worth[25] has observed that the pupil contracts in a newborn infant if a light is suddenly flashed on to its eye in the dark, and that the child will try to fix it for an instant, as by a reflex act, showing that some preponderance in power at the macula is innate. He says: "At the end of two or four weeks most infants will fix a light steadily for several seconds at a time with one or other eye, but will not converge both visual axes accurately in looking at a near object. It is not until five or six weeks that binocular fixation manifests itself."

The high acuity of form-sense at the fovea may be due to:

(*a*) The close congregation of cones together in that region.

(*b*) The isolation of each cone in that region to one nerve path.

(*c*) The opening out of the inner layers of the retina, allowing the unimpeded access of rays of light to the cones.

Probably all three factors are essential for clearness of definition in vision.

If, as suggested in the consideration of the light-sense, the response of the cones to light is a mechanical one, a contraction produced in one of them being capable of starting a stimulus in the isolated nerve path with which it is connected, we have a very simple means of explaining the first stage in the production of the perception of form.

At the center of the fovea in the human retina we have an area in which 7000 cones are supposed to be crowded together; 50 cones may be counted along a line of 200 μ in length; the average diameter of each cone at its widest part is about 3 μ, and the distance between two adjoining cones 4 μ. Supposing now the image of a black letter on a white ground, such as we have in our test-types, to be focussed on this delicate mosaic of cones, those upon which the white background is projected will be stimulated and contract, those upon which the black letter fell, not being stimulated, will remain uncontracted. Indeed, it seems likely that if we could examine the outer surface of a retina so stimulated, under sufficient magnification, a reproduction of the letter looked at would be seen raised up and composed of the unretracted outer limbs of the cones.

An abnormally low acuity of central form-sense dating from birth, and unaccompanied by any obvious ophthal-

moscopic changes, might be due to an absence of any one of the three above-mentioned characteristic features at the macula, so that the condition we describe as "congenital amblyopia" might be brought about in different ways; we have, however, definite anatomical evidence that in connection with it the fovea is sometimes found to be absent.

Seefelder[26] recorded the absence of the fovea in a case of congenital amblyopia and nystagmus associated with aniridia. Its absence has also been noted in congenital amblyopia accompanying albinism. Further investigations as to the structure of the retina at the macula in connection with congenital amblyopia is, I suggest, much to be desired.

Monkeys, the class of mammals which first developed a fovea, like birds, in whom a fovea is almost always present, live an arboreal life. They, like birds, subsist on a diet of fruit and insects, which has to be picked up, picked off or picked out. This picking process requires considerable concentration and sharpness of vision. In the case of birds it is done with the bill, and in the case of monkeys with the fingers.

Other mammals who have adopted the arboreal habit, such as lemurs, some of the Insectivora and rodents, have not developed a fovea, the reason probably being that they make more use of their teeth and comparatively elongated snouts for the picking up and preparation of their food than the higher Primates, and therefore require less acuteness of vision for detail.

The adoption by monkeys of feeding habits, intimately associated with the use of the hands and the formation of a central spot of acute form-sense, endowed them with the capacity of picking up objects and examining them closely. Such a capacity would tend to excite feelings of curiosity, the marked development of which is one of the characteristics

of all apes, and from this would arise a desire for investigation. It must have been the overpowering influence of such a desire which induced man's ancestors to descend from the safety of the branches to explore the earth beneath, and thereby encounter new and unknown dangers. The appetite for exploration and research, thus started, grew by what it fed on, and continues to grow even up to the present time.

CHARTER IV.

ACCOMMODATION AND CONVERGENCE.

INTIMATELY associated with the evolution of the fovea centralis, and therefore with the adoption of arboreal life, is an increased capacity for accommodation and convergence.

The accommodative power of the eyes of mammals has been investigated by several different observers. All are agreed that its range is greatest in man, slightly less in apes, and very considerably less in all the lower orders.

Hess and Heine[27] found its range equal to 10 to 12 D. in apes; 2.5 to 3.5 D. in dogs; 1.25 D. in cats; 2.5 to 3 D. in a young wolf; and 0 in rabbits.

Barrett[28] was unable to detect any alteration of refraction, during examination by retinoscopy or with the ophthalmoscope, in any mammal except man and monkeys. Those which he examined were rabbits, guinea-pigs, rats, mice, cows, horses and dogs among domestic animals; and deer, jackal, pecari, various cats, hyena, opossum, porcupine, mongoose and thirteen monkeys among wild animals. He found that electrical stimulation of the eyes of cats and dogs produced no result, and that the voluntary accommodation of monkeys was equal to 4 to 5 D.

Beer[29] estimated the range of accommodation in *Macacus rhesus* as equal to 10 D., and that in the anthropoid and some other apes it was still greater, approaching even in the untailed apes to the degree present in man. By electrical stimulation of the freshly enucleated eye of the common cat

he observed an increased projection of the anterior surface of the lens, but the increased refraction amounted only to 2 or 3 D. In the solipedes and ruminants he estimated the range as from $\frac{1}{2}$ to 2 D. In the hare and rabbit he totally failed to discover any change, either after administration of miotics or after electric stimulation.

FIG. 9.—Ciliary body of the echidna.

Priestley Smith,[30] by examining rabbits' eyes with the shadow test and the faradic current, convinced himself that there was some accommodative change, though in several it was slight and very transient.

In the horse and dog and probably in most wild mammals the refraction is hypermetropic, so that, their accommodation being feeble, their near point cannot be nearer than one or two meters away. Barrett thoroughly atropinized

the eyes of a cat and then allowed it to pursue a mouse, which it caught without any difficulty.

I have examined microscopically sections of the ciliary body from the eyes of mammals belonging to various different natural orders, and find that the degree of development of the ciliary muscle corresponds fairly accurately with the degree of capacity for accommodation which the animal has been found to possess.

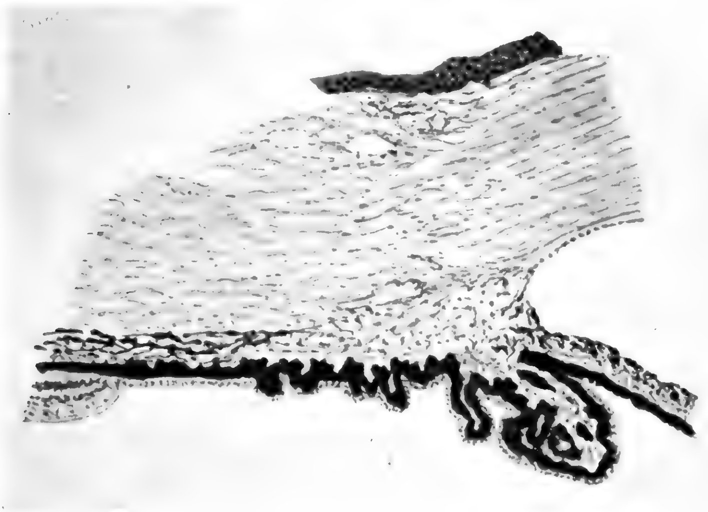

FIG. 10.—Ciliary body of the great ant-eater.

In some of the lowest mammals, such as the echidna (Fig. 9) and the great ant-eater (Fig. 10), the ciliary muscle is practically non-existent. In rabbits (Fig. 11) only a few scanty fibers are recognizable. In the marsupials (Fig. 12) there is a small definite bundle of longitudinally placed fibers. In the Ungulata (Fig. 13) and Carnivora (Fig. 14) the longitudinally directed fibers are more numer-

ous and form a considerably broader band. The ciliary muscle in apes (Figs. 15 and 16) and man shows an extensive

FIG. 11.—Ciliary body of the rabbit.

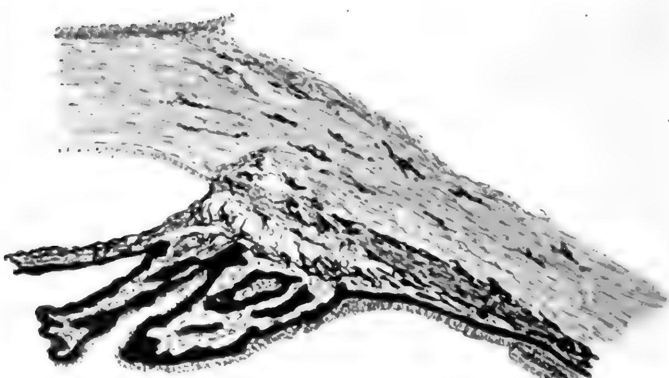

FIG. 12.—Ciliary body of the wallaby.

increase in development on that met with in any of the other mammals. Not only is it wider and longer, but its

fibers show a more complex arrangement. In all the other mammals which I have examined it is composed entirely of longitudinal fibers; in apes and man it possesses also what have been described as radial and circular fibers (Fig. 17).

FIG. 13.—Ciliary body of the ox.

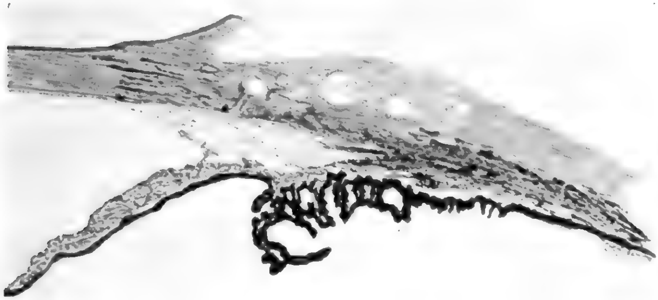

FIG. 14.—Ciliary body of the cat.

At the International Ophthalmological Congress held at Utrecht in 1899, I demonstrated how the arrangement of the ligamentum pectinatum also differs very considerably

in man and apes from that met with in other mammals. In the human eye the fibers of which it is composed radiate out in a fan-like fashion from the position where Descemet's membrane ends, and the angle of the anterior chamber is prolonged outward 0.8 mm. beyond that point. So that if a line vertical to the surface of the eye be drawn back-

FIG. 15.—Ciliary body of the Rhesus monkey.

ward through the canal of Schlemm it passes into the angle of the anterior chamber (Fig. 17). If the same line be continued backward it almost passes through the large circular artery at the base of the iris, and only a small portion of the ciliary processes lie to its inner side. In the lower mammals the ligamentum pectinatum is a much more

extensive structure, filling up a large part of what forms the angle of the anterior chamber in the human eye It is composed of an external laminated zone, attached on its

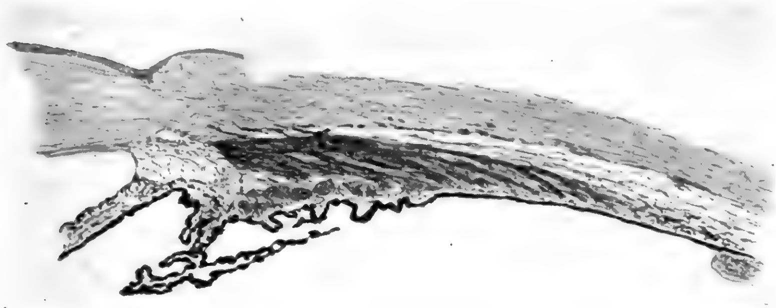

FIG. 16.—Ciliary body of the chimpanzee.

outer surface to the sclerotic, which is wider and more spaced out than in the human eye, and an inner cavernous zone

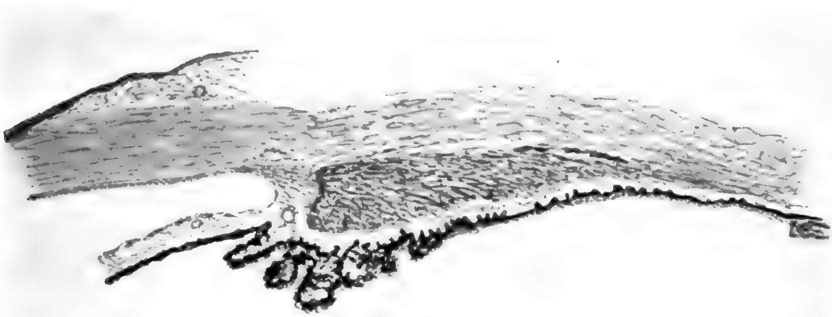

FIG. 17.—Ciliary body of the human eye.

with irregularly shaped spaces between its fibers (Fig. 13). The inner limit of the ligament, that facing the anterior chamber, in these animals, is bounded in places by what

are called the pillars of the iris. These consist of prolongations forward of the stroma of the iris to the back of the cornea, to which they are adherent just where Descemet's membrane terminates (Figs. 11 and 12). It is these bands of iris tissue, which are not present in man's eye, that give the toothed appearance to the ligament, and which led to its being compared to a comb. It is the disappearance of these pillars of the iris in man's eye which has allowed the anterior part of the ciliary body to become displaced backward. As the angle of the anterior chamber in the lower mammals does not extend beyond the point where Descemet's membrane ends, a line drawn backward vertically to the surface of the eyeball through the canal of Schlemm does not pass through the angle of the anterior chamber but some distance external to it, and the large circular artery of the iris, together with a large portion of the ciliary processes, lies to its inner side (Figs. 13 and 14).

The concentration of the fibers of the ligamentum pectinatum together in the human eye forms a fixed point, or tendon of origin, for the ciliary muscle. In the lower mammals, where the area occupied by the ligamentum pectinatum is broader and more spaced out, the fibers of the ciliary muscle do not have any fixed point of origin. Running longitudinally they terminate anteriorly in the spaces between the fibers of the ligamentum pectinatum, in the same way as they terminate posteriorly between the fibers of the lamina suprachoroidea (Fig. 14).

A comparison of the ciliary muscle in its different degrees of development in different mammals shows that the spindle-shaped cells of which it is composed lie between the fibers of the lamina suprachoroidea.

In the human eye the fibers of the lamina, if traced forward, can be seen to enter the posterior border of the ciliary

muscle, so that the most anterior portion of the perichoroidal space is entirely free from any such fibers. If the uvea be separated from the sclerotic some of the anterior and external of the cells of the ciliary muscle may be found attached to the latter coat, being situated between the layers of what elsewhere forms the lamina fusca.

In some animals, as pointed out by Kalt, at the termination of the ciliary body posteriorly, in the spaces of the lamina suprachoroidea left empty by undeveloped muscle fibers, a layer of large cells is met with continuous behind with the endothelial cells of the choroid.

In pathological specimens, where, as the result of edema of the ciliary body, or as the result of traction from fibrous bands on its inner surface, its tissue has been much spaced out, I have met with large cells between the muscle fibers, suggesting in their appearance transitional stages between endothelial cells and muscle cells.

Muscle fibers, or at any rate cells which cannot be distinguished from them, are met with in isolated patches of the external surface of the choroid; thus Salzmann[31] writes: "If one follows the suprachoroidea from behind forward new structural elements, smooth muscle fibers, appear even in the equatorial region, or, at times, still farther posterior, therefore in the territory of the choroidea. They are grouped in bundles singly, or for the most part branched, and then forming three or more rayed stellate little figures—'muscle stars.'"

Fuchs,[32] in a recent article, has described how he found muscle fibers in the lamina suprachoroidea in the neighborhood of the papilla in frontal sections through the optic disk.

The above facts, taken together, all tend to show that the spindle-shaped cells composing the ciliary muscle are

morphologically the same as the endothelial cells found in the spaces of the lamina suprachoroidea and in the pectinate ligament, and that the development of the ciliary muscle is due to the proliferation and lengthening out of such endothelial cells.

Anatomists have frequently described Descemet's membrane as the uveal layer of the cornea, and I think such a description is both accurate and useful. Descemet's membrane is composed of the same elastic tissue as that of the pectinate ligament, both staining in a similar way with acid orcein. Elastic fibers are also found in the lamina suprachoroidea. The elastic tissue of Descemet's membrane has been proved to be produced as a kind of secretion of the endothelial cells lining it. In the human fetus, before the iris is formed, and before there is any anterior chamber, two parallel rows of cells are seen lying interposed between the cornea and the anterior capsule of the lens. The anterior chamber is developed as a space between these two rows of cells, the anterior of which becomes the lining endothelium of Descemet's membrane, and the posterior the endothelium on the surface of the iris and of the pupillary membrane. It may therefore be claimed that not only does Descemet's membrane represent the uveal layer in the cornea, but that the anterior chamber is analogous to an opened-out and enlarged potential space of the lamina suprachoroidea.

These morphological analogies of the fibers of the ciliary muscle and its surroundings are of considerable assistance in understanding the distribution of its fibers in the human eye. Having recognized that the fibers of which the muscle is composed are developed from cells contained in spaces on the outer surface of the ciliary body, it becomes evident that the shape and direction of these muscle fibers will depend on that of the spaces in which they are formed.

In all mammals in which the ciliary muscle is rudimentary its fibers run longitudinally (Figs. 11, 12, 13 and 14). It is only when we come to the more highly developed ciliary muscle of Primates that we meet with the addition of radial and circular fibers internal to the longitudinal ones (Figs. 15, 16 and 17). It is in these animals also that we meet with a considerable displacement backward of the anterior part of the ciliary body, due to disappearance of the pillars of the iris, and alteration in the arrangement of the fibers of the pectinatum already referred to. The ciliary processes in Primates, instead of projecting out from the back of the iris, have become displaced outward and backward beyond its root, thus altering the shape and direction of the lymph spaces immediately external to them. The innermost of these spaces assume a circular direction, and those more external a radial course; the muscle fibers developing in these spaces from the cells lining them take the same direction.

Donders[33] pointed out that the construction of the ciliary muscle varies with the refractive condition of the eye. He found that in actual myopia it was flatter and longer than in emmetropia or hypermetropia, and that its point of origin from the fibers of the ligamentum pectinatum was situated farther back.

Iwanoff[34] described how, in myopia, the ciliary muscle consists almost entirely of longitudinal fibers, "Brücke's muscle," the circular fibers, "Müller's muscle," being absent, while in hypermetropia he found that the circular fibers were more numerous than in emmetropia, and formed a considerable inward projection from the anterior part of the muscle. This inward projection of the muscle is accompanied by an inward projection of the ciliary processes behind the root of the iris. In myopia the ciliary processes

are much less prominent, and are separated by a considerable distance from the root of the iris (Fig. 18).

No doubt, as has frequently been pointed out, the ciliary muscle in hypermetropia, having more work to do, is hyper-

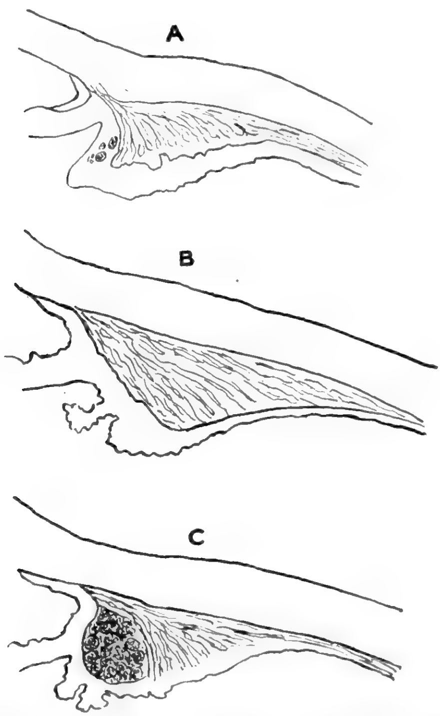

FIG. 18.—Varieties of the ciliary muscle. *A*, emmetropic; *B*, myopic; *C*, hypermetropic. (From Iwanoff.)

trophied, while in myopia, having but little work to do, it is atrophic. I think, however, the direction of its fibers is largely influenced by the length of the antero-posterior axis of the eyeball. Where this has been abnormally increased, as in axial myopia, the uveal tissue is considerably

stretched, the ciliary processes are drawn backward, and the spaces in the tissue immediately external to them are also drawn backward and elongated out. The fibers of the ciliary muscle contained in these spaces become likewise altered in their direction, and assume a longitudinal position antero-posteriorly instead of running circularly.

In hypermetropia, where the eyeball is abnormally short from before backward and not fully developed, the ciliary processes, as in the embryonic condition and as in the lower animals, project farther forward and inward, so that the spaces external to them, and the muscle fibers contained therein, have a circular direction.

In animals below Primates in which the ciliary muscle has scarcely any more fixed point of attachment anteriorly than it has posteriorly, and where its fibers have all a longitudinal direction, the effect of their contraction would appear to produce a drawing together, or rucking up, of the inner surface of the ciliary body, much in the same way as contraction of the dilator muscle fibers of the iris draws together or rucks up the iris in dilation of the pupil (Fig. 14). In apes and in man the concentration together of the fibers of the pectinate ligament at the sclero-corneal margin produces a sort of tendon, or fixed point of origin, to the ciliary muscle. So that on its contraction the tissue into which it is inserted is drawn forward toward this fixed point.

A study of the morphology and embryology of the lens and its suspensory ligament seems to leave no doubt that the effect of contraction of the ciliary muscle is, as Helmholtz pointed out, a slacking of the suspensory ligament and a relaxation of tension in the lens fibers.

The following table gives the measurements of the antero-posterior and lateral diameters of the lens in the eyes of several different mammals:

DIAMETERS OF THE LENS IN MAMMALS.

	Antero-posterior.	Lateral.
Man	4.5 mm.	9 mm.
Chimpanzee	4 "	7 "
Monkey	3.5 "	6 "
Civet cat	5 "	6.5 "
Virginian fox	6 "	8 "
Horse	11 "	20 "
Antelope	11 "	14 "
Sheep	10 "	12.5 "
Pig	6 "	9 "
Rabbit	7 "	9 "
Rat	4 "	4.5 "
Hedgehog	3.5 "	3.5 "
Sooty phalanger	7 "	9.5 "
Great ant-eater	6 "	8 "
Rat kangaroo	8 "	10 "

From this it will be seen that in man the antero-posterior diameter of the lens measures nearly half that of the lateral diameter. In monkeys it is a little more than half, while in all the other mammals the proportional difference between the two diameters is considerably less, and in some of them the lens is almost spherical (Fig. 19).

In man and monkeys the ciliary processes are separated from the sides of the lens by a definite space—the so-called circumlental space. In all other mammals the ciliary processes lie in contact with the sides of the lens.

It seems natural to infer that the flattening of the lens from before backward in man's eye has resulted from the growth of the ciliary body away from the sides of the lens, and the traction which is thereby produced on its anterior and posterior capsule through the suspensory ligament. An examination of embryonic human eyes in different stages of development confirms this view. The ciliary processes, when first formed, are in contact with the sides of the lens, and with the growth of the eyeball gradually become separated from it. In association with the gradual

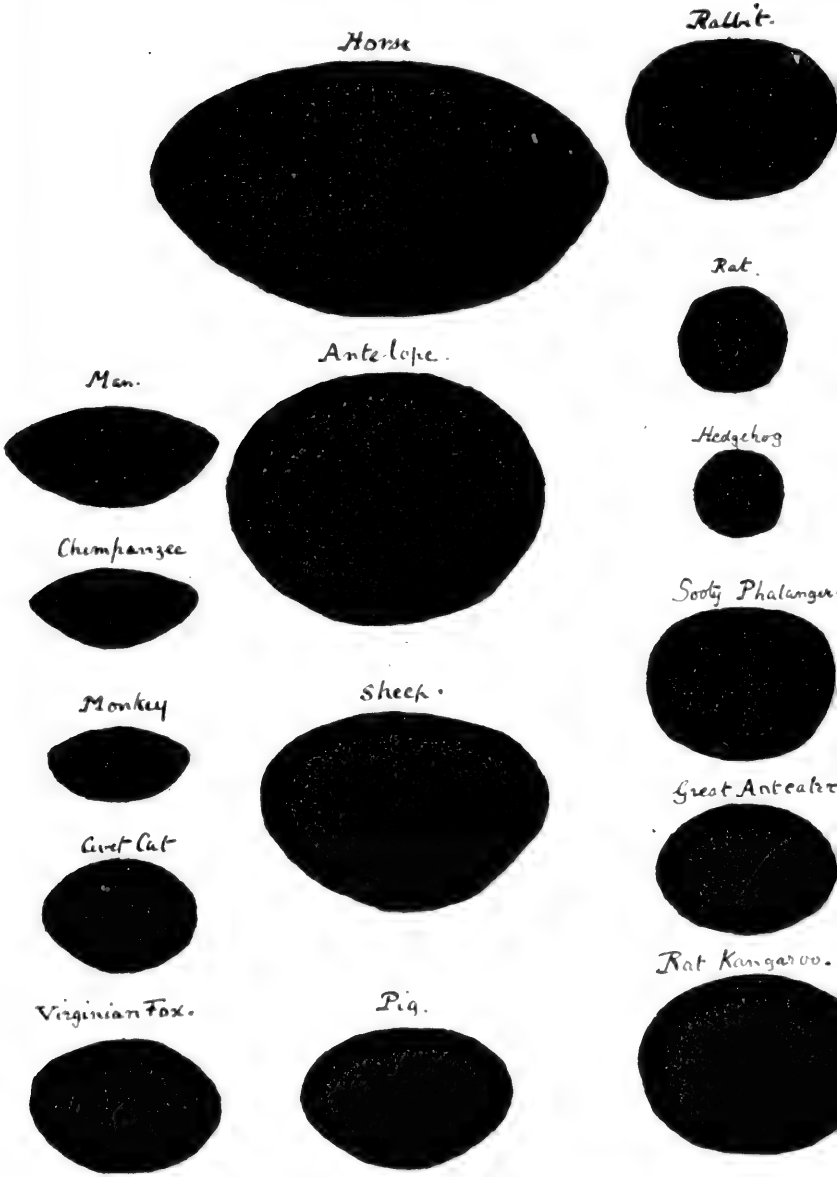

FIG. 19.—Lenses in mammals drawn three times natural size.

separation of the two structures there is alteration in the shape of the lens from that of a sphere to that which it assumes in the fully formed eye.

The following table gives the measurements of the antero-posterior and lateral diameters of the lens in a series of human fetal eyes of different ages, and those recorded by Dub[35] from the ninth month to the twelfth year:

Age.	Antero-posterior.	Lateral.
Fourth month	2.8 mm.	3.3 mm.
Fifth "	3.5 "	4 "
Sixth "	3.8 "	4.5 "
Seventh "	4 "	5 "
Ninth "	4.3 "	5.75 "

To these may be added those given by Dub from the ninth month to the twelfth year:

Age.	Antero-posterior.	Lateral.
9 to 12 months	2.46 mm.	7.46 mm.
1 to 2 years	2.57 "	7.87 "
2 to 3 "	2.72 "	8.2 "
3 to 4 "	2.83 "	8.46 "
4 to 5 "	3.0 "	7.8 "
5 to 6 "	3.2 "	8.4 "
7 "	2.9 "	8.2 "
12 "	3.6 "	8.8 "
Adult	4.5 "	9 "

From this it will be seen that the lens, when first formed, is spherical in shape, and gradually assumes its flattened condition with the growth of the eyeball. After birth the traction on the sides of the lens causes a diminution in its antero-posterior diameter (Fig. 20).

If further confirmation is required that flattening of the lens and consequent bowing of its fibers occurs, as the result of traction on its sides, it is to be found in the effects of pathological enlargement of the eyeball, such as occurs in cases of congenital glaucoma—so-called buphthalmos. In

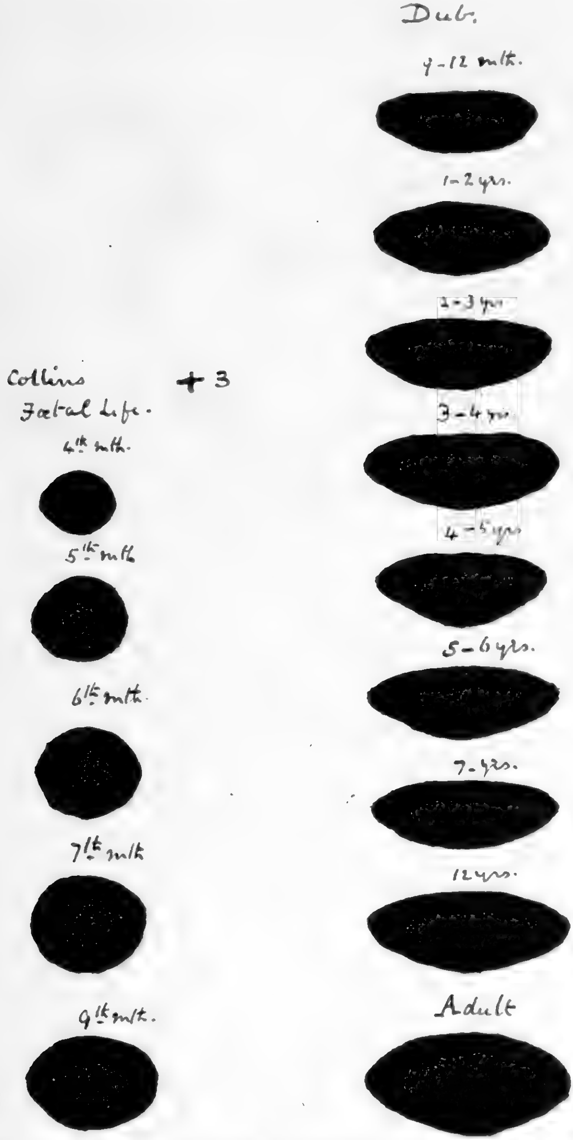

FIG. 20.—Lenses in human eyes at different ages, drawn three times natural size.

this disease there is considerable expansion of all the diameters óf the eyeball, and considerable widening of the ciliary region, so that the ciliary processess become separated farther than normally from the sides of the lens, and the circumlental space is increased in width. At the same time the antero-posterior diameter of the lens is diminished and the lateral diameter increased. In one specimen which I have the antero-posterior diameter of the lens measures 3.5 mm., the lateral 9 mm., and in another the antero-posterior diameter is 4 mm. while the lateral is 10 mm.

Investigations into the anatomy of the suspensory ligament of the lens have shown that it is composed of separate bundles of fibers, which run in different directions, and to which specific names have been attached. The two chief bundles are: The orbiculo-antero-capsular fibers, lying in the valleys between the ciliary processes, which attach the posterior non-plicated part of the ciliary body to the anterior capsule of the lens; and the cilio-postero-capsular fibers, passing between the bundles of orbiculo-antero-capsular fibers, which attach the anterior part of the ciliary processes to the posterior capsule of the lens. A third set of fibers—the equatorial—attaches the center of the ciliary body to the side of the lens capsule.

To understand how these different bundles of fibers of the suspensory ligament are developed, it is necessary to examine the relations which the ciliary body, or the part of the eye which ultimately becomes the ciliary body, bears to the side of the lens at different periods of fetal life. For some time the two structures lie in contact, and it is while they are in contact that adhesions form between them, which ultimately develop into the fibers of the suspensory ligament. At an early stage of fetal life, before the iris and ciliary processes have commenced to form, the part of the

globe where the non-plicated part of the ciliary body ultimately develops lies in contact with the anterior capsule of the lens, and forms adhesions to it (Fig. 21, *A*). On

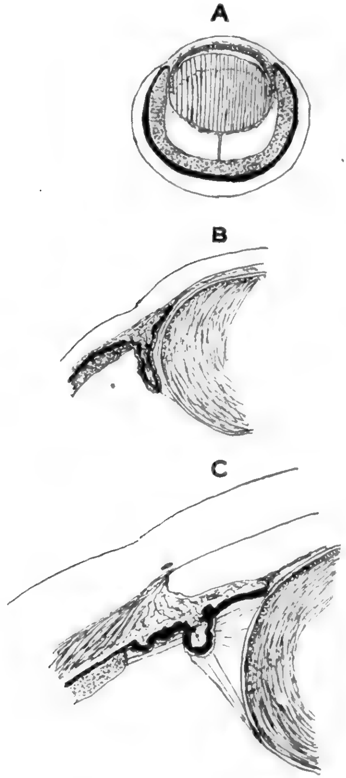

FIG. 21.—Diagram to show relation of ciliary body to the side of the lens at different times in fetal life.

the growth of the globe this part of the ciliary body gradually recedes, the ciliary processes budding out in front of it. The direction in which the ciliary processes grow is at first inward and backward, so that they come to lie in contact

with the posterior capsule of the lens, and while there form adhesions to it (Fig. 21, *B*). On the expansion of the globe the ciliary processes become separated from the sides of the lens—a separation which is still further increased on the formation of the anterior chamber, which displaces the lens backward (Fig. 21, *C*). The growth of the ciliary body away from the side of the lens causes the adhesions which have formed between them to be lengthened out into the fibers of the suspensory ligament. It also, by exerting traction on the anterior and posterior capsule and sides of the lens, causes that structure to alter its shape, so that it loses its spherical form and becomes flattened antero-posteriorly; the flattening is more marked on the anterior surface than the posterior because the traction is greater on the anterior capsule than the posterior, due to there being a wider separation of the non-plicated parts of the ciliary body from the anterior capsule of the lens than of the ciliary processes from the posterior capsule. Flattening of the lens antero-posteriorly, due to traction on its anterior and posterior surfaces, increases the curve of its fibers, and keeps them so curved until the traction on the two surfaces is relaxed, *i. e.*, until the suspensory is rendered slack by the contraction of the ciliary muscle. The effect of such slackening must necessarily be most on the anterior surface upon which the traction is greatest, and most of all in the central circular area on the anterior surface around which the most anterior of the fibers of the suspensory ligament are attached.

The farther the backward growth of the non-plicated part of the ciliary body, with the orbiculo-antero-capsular fibers attached to it, the greater will be the traction on the anterior capsule of the lens and the increase of latent accommodative power. One of the features in the architecture

of the eye in man and monkeys, which is strikingly distinctive from that in lower mammals, is the elongation of the pars plana of the ciliary body, *i. e.*, the region situated between the hindermost of the ciliary processes and the ora serrata. This is brought out to some extent in the following table, which shows in a series of mammals' eyes the length of a straight line drawn between the root of the iris and the ora serrata in one column and the antero-posterior diameter of the eyeball in the other:

	Antero-posterior diameter of eyeball. mm.	Distance between root of iris and ora serrata. mm.
Man	24.8	6
Chimpanzee	19	4.25
Rhesus monkey	19.5	5
Capuchin monkey	18.5	4.25
Cat	22	3.5
Horse	44	5 to 10
Ox	35	6.5
Antelope	27	3 to 5
Sheep	28	3 to 6
Pig	22	4
Rabbit	19	2

In the Ungulata two measurements are given, because in animals with horizontal oval pupils the distance of the root of the iris from the ora serrata is considerably less where the iris is narrow than where it is broad.

From this table it will be seen that in man and monkeys the distance between the root of the iris and the ora serrata is about one-quarter of the antero-posterior diameter of the globe, while in all other mammals, except the Ungulata, it is considerably less. In the Ungulata, while it measures nearly one-fourth in the vertical diameter, it is considerably less in the lateral.

A lens flattened antero-posteriorly has considerably less refractive power than a spherical or nearly spherical one. The lesser refractive power of the lens in man and monkeys, due to flattening of it antero-posteriorly, is to some extent

compensated for, as already mentioned, by increased refractive power in the cornea. Further compensation is effected by increase in the depth of the vitreous chamber and displacement backward of the retina, on which the image of the object looked at has to be focussed. The following table gives the depth of the vitreous chamber from the posterior pole of the lens directly backward to the retina, and the diameters of the lens, in a series of mammalian eyes. From this it will be seen that a decrease in the sphericity of the latter is accompanied by an increase in the depth of the former.

		Lens.	
	Vitreous chamber.	Antero-posterior.	Lateral.
Man	15.4 mm.	4.5 mm.	9 mm.
Chimpanzee	11.5 "	4 "	7 "
Horse	20 "	11 "	20 "
Antelope	12 "	14 "	17.5 "
Pig	9 "	6 "	9 "
Rabbit	6 "	7 "	9 "

Thus, while in the rabbit and antelope the depth of the vitreous chamber is less than the width of the antero-posterior diameter of the lens, in the horse and pig it is considerably greater. In man and the chimpanzee the depth of the vitreous chamber is nearly three times as great as the width of the antero-posterior diameter of the lens.

A similar comparison may be made in the changes which take place in the shape of the lens and in the depth of the vitreous chamber during the process of development of the human eye. The following table shows the depth of the vitreous chamber and the diameters of the lens of the developing human eye up to the time of birth.

		Lens.	
Age.	Vitreous chamber.	Antero-posterior.	Lateral.
Fourth month	4.5 mm.	2.8 mm.	3.3 mm.
Sixth month	5 "	3.8 "	4 "
Seventh month	7.5 "	4 "	4.5 "
Ninth month	9.5 "	4.3 "	5.75 "
At birth	11 "	3.75 "	7 "

Weiss[36] has shown that the anterior segment of the eyeball grows rapidly during the first year of life and attains its full dimensions by the end of the second year. The subsequent growth of the eye, which continues into the twenties, is entirely due to an expansion of the posterior segment. At birth the depth of the vitreous is 11 mm. and in the adult eye 15.4 mm.

This difference in the depth of the vitreous chamber in different classes of mammals, and at different periods in the course of development in man's eye, may be correlated with the varying states of refraction met with.

The refraction of the eyes of a large number of mammals has been investigated by Lang and Barrett[37] and by Lindsay Johnson.[3] Their investigations agree in showing that wild species of mammals are always hypermetropic. Lindsay Johnson says: "A slight degree of hypermetropia, *i. e.*, under 1 D. may be said to be the rule throughout the higher mammals, while higher hypermetropia, *i. e.*, 2 D. to 5 D., is found in the wild species of rodents, the Edentata and the Marsupials."

Among domesticated mammals myopia is not uncommonly met with. In a series of mammals Lang and Barrett found it in the following proportions of the eyes examined: Rabbits, 5 out of 52; guinea-pigs, 5 out of 28; rats, no myopia, but 1 mixed astigmatism out of 10; cows, no myopia in 10; horses, no myopia, but 1 mixed astigmatism out of 6; cats, 2 out of 12; dogs, 2 slight myopia out of 6. Lindsay Johnson says: "Myopia is frequently met with both with and without astigmatism among domesticated animals, especially guinea-pigs, rabbits and other rodents kept in confinement in small hutches." He also states that he found myopia to be a persistent characteristic in mandrils and baboons. Lang and Barrett found that 2 monkeys out of 11 which they examined were myopic. There is no note as to how long

these myopic monkeys had been kept in confinement previous to having their refraction tested.

The tendency to the development of myopia as an outcome of confinement in restricted spaces seems to be an example of adaptation of structure to function, *i. e.*, an elongation of the posterior part of the eyeball to meet requirements of vision for near objects. It is similar to the condition of things which is met with in human beings. The incompletely developed eye of the newborn is nearly always hypermetropic, the mean amount met with having been estimated by different observers as 2.3 D. and 3 D. During the first decade of life the hypermetropia curve rapidly falls, while the percentage of myopes increases during the first two decades.

Man's eyes at birth are comparable to those of terrestrial mammals in the natural state, who have not adopted arboreal life. His lenses are then nearly spherical and his vitreous chambers of comparatively little depth, so that his eyes are adapted for vision at long distances, with but little capacity for the focussing of near objects. By expansion of the globes, flattening of the lenses antero-posteriorly and increase in the depth of the vitreous chambers, man's eyes gradually reach that condition which is most suitable for his environment under normal conditions, *i. e.*, where parallel rays are brought accurately to a focus on the macula when the ciliary muscle is at rest, and where there is an ample capacity of accommodation for near objects. If, while this developmental process, which lasts up to the twentieth year, is still proceeding, man's vision becomes unduly restricted to use at short ranges, then, as in the lower mammals which are kept confined in small compartments, adaptation of structure to function tends to take place, the vitreous chambers become deeper than normal and myopia is developed.

As already pointed out, the development of a highly acute spot of central vision for form-sense is correlated in mammals with a change in feeding habits, viz., the use of the hands for picking up food and conveying it to the mouth, instead of in the first place seizing it with the mouth. When the food consists of small things, such as fruits, grains, nuts and insects, acute form-sense, unless accompanied by active accommodative power, would be of very limited use. Hence, like the development of the fovea centralis, the increased range of accommodation, which has necessitated the extensive changes in the shape and structure of the eye just mentioned, has been the outcome of the adoption of arboreal life.

Just as we find the development of active accommodation linked up with the development of acute central form-sense, so we find the power of convergence linked up in its formation with the development of active accommodation. Indeed, these three visual factors appear to have evolved, *pari passu*, with life in the trees.

As has already been pointed out, the evolution of conjugate movements of the eyes is associated with the presence of semi-decussation of the fibers of the optic nerves at the chiasma, the receipt of visual impressions from the two eyes on the same side of the brain, and the development of corresponding points in the retina. These conjugate movements reach to a high degree of perfection in the Carnivora, but it is only when we come to the Primates that we meet with a highly developed power of convergence in association with stereoscopic vision.

Some reptiles and birds are able to converge the axes of the two eyes on objects when feeding, but they have complete decussation of the fibers of the two optic nerves. Visual impressions from the two eyes are not received in them on the same side of the brain, so that they do not have true

stereoscopic vision. A movement of the eyes may be observed in some of the Ungulata, when their attention is suddenly attracted, which is an approach toward convergence, but which is really more a movement from divergence toward parallelism. It is exceedingly well depicted in a plate in Chalmers Mitchell's book on *The Childhood of Animals*, which shows a group of spring-bok facing the artist, in the characteristic attitude of attention, at the London Zoölogical Gardens a few hours after a kid was born. In the Carnivora more obvious attempts at convergence may be noted; when holding food with their front paws they tear it with their teeth. Dogs can be trained to converge by having a lump of sugar placed on their nose "on trust."

The associated evolution of acute central form-sense, accommodation and convergence, is of considerable interest when we consider the intimate dependence of each one upon the others for purposes of stereoscopic vision. If any one of these three faculties becomes seriously interfered with, so that the balance between them is disturbed, then the recently acquired capacity of fusing the images seen with the two eyes is given up, and one eye only is employed for fixation, the other being allowed to wander in the direction of least resistance, the condition we speak of as concomitant strabismus being established. Concomitant strabismus may be the outcome of several different causes, but three well-established predisposing factors are: (1) A defect in the development of the central form-sense in one eye, *i. e.*, congenital amblyopia; (2) the presence of hypermetropia, which leads to an excessive amount of accommodative effort being made in the focussing of the images of near objects; (3) the presence of heterophoria, which leads to undue amount of effort on the part of the recti muscles to maintain the requisite amount of convergence.

CHAPTER V.

COLOR-SENSE.

THE color-sense of mammals has been investigated by experiments and by a study of their natural history. I propose briefly to summarize the conclusions these investigations have led to, discuss the way in which the color-sense has been influenced by the adoption of arboreal life, and endeavor to correlate its varying degrees of acuteness with the different anatomical appearances met with in the percipient end-organs of the retina.

Many carefully thought-out experiments have been performed to test the chromatic sense in mammals, and in some elaborate precautions have been taken to exclude any fallacy which might be occasioned by unequal degrees of luminosity. These experiments have mostly been applied to dogs and monkeys. The details of them will be found well epitomized in Parsons'[17] book on *Color Vision.* It will suffice for my purpose here to quote only the results obtained.

Graber[38] found that the pig and the dog could distinguish between blue and red, showing a distinct preference for the former; it is, however, doubtful if this preference was not due to brightness rather than color.

Kalischer[39] came to the conclusion, from feeding experiments he carried out on dogs, that there is no doubt of their ability to perceive differences of hue as well as differences of brightness; but that there exist considerable differences in their sensibility to color.

Miss E. M. Smith,[40] from an elaborate series of experiments on dogs, summed up her conclusions as follows:

"1. That while evidence has been obtained to show that some dogs possess a rudimentary power of color discrimination, such discrimination is highly unstable and cannot be supposed to play any part in the animals' normal existence.

"2. That the color-sense is, as shown by the high color threshold, very weak.

"3. That color discrimination, even where clearly established, may be readily inhibited by differences of luminosity or position."

Kinnaman[41] carried out experiments on monkeys with food in glass tumblers covered with different colored cards, and came to the conclusion that their capacity to distinguish color as such was undoubted.

Dahl[42] colored some sweets and some bitter substance with different colored dyes; he found that after a few attempts a monkey learned to leave without even tasting those which were colored with the dye indicating a bitter substance, and to seize at once upon those colored to indicate sweets. Varying the experiments sufficiently he found that the monkey distinguished all the different colors readily except dark blue.

Hess[43] tested a monkey in the following manner: Grain was scattered over a black surface upon part of which a spectrum was thrown. The monkey gathered all the grains from the extreme red to the extreme violet, leaving those unilluminated. When the animal was dark-adapted and the intensity of the light diminished until the grains were visible to the dark-adapted experimenter only in the yellow and green, only those grains were gathered. Hess concludes that the extent of the spectrum is the same for the

monkey as for man, and that it is brightest for the dark-adapted monkey in the region where it is also brightest for the dark-adapted man.

From the results obtained by these various experimenters it seems evident that the color-sense of monkeys is much the same as in man, but that that of dogs and of other mammals experimented on is much less highly developed.

The origin of the color-sense and of the coloring of animals received much attention from the great pioneers of evolution of the last century—Darwin, Alfred Russell Wallace, Lubbock and Grant Allen. Much of what they wrote, brings out very clearly what I am now endeavoring to show, viz., that the color vision of Primates is far more acute than that of other mammals, and that this is due to their arboreal life with its natural accompaniment of a frugiferous diet. I cannot do better than quote from their writings, especially from Grant Allen's[44] fascinating book on *The Color Sense: its Origin and Development*, which has not, I think, attracted the amount of attention which it deserves. What is to be learned regarding the color-vision of mammals from a study of their natural history he sums up as follows:

"When we come to the highest class of vertebrates—the Mammalia—strangely enough the evidence of a color-sense almost fails us. The antipathy of male ruminants for scarlet and the curiosity which certain monkeys display with regard to bright-colored objects are the only facts in point which come under ordinary observation. This result, so contrary to what we might have expected, appears quite natural when we examine more closely the circumstances of the case. By far the larger part of the mammals are herbivorous like the ruminants and pachyderms, or carnivorous like the technical carnivores, insectivores and whales. Only a small portion of the class subsists

upon fruits, while none of them are very specially connected with flowers. Hence a large set of possible tests which we can employ in the case of insects and birds are wholly inapplicable to mammals. Moreover, the want of close relations with the colored parts of plants has probably resulted in a want of any peculiar love for bright color, such as we see reason to suspect in the butterflies, humming-birds and parrots. This absence of taste for brilliancy is probably marked by the absence of brilliant hues in the animals themselves; the result of sexual selection for these hues, as we shall see hereafter, only appears among the Mammalia in a few higher arboreal and frugivorous species such as the mandril and certain squirrels."

Alfred Russell Wallace,[45] in discussing the origin of the color-sense, said: "The primary necessity which led to the development of the sense of color was probably the need of distinguishing objects much alike in form and size but differing in important properties, such as ripe and unripe or eatable and poisonous fruits, flowers with honey or without, the sexes of the same or of closely allied species. In most cases the strongest contrast would be the most useful, especially as the colors of the objects to be distinguished would form but minute spots or points when compared with the broad masses of tint of sky, earth or foliage against which they would be set."

The association of brilliant hues in the external coverings of animals with those of the objects from which they obtain their food is very striking. Humming-birds, which are the most highly colored of all birds, obtain their food from flowers; they have a bifid tubular tongue which they insert into the corolla of flowers to suck up the honey. Parrots, whose plumage is generally extremely bright and gaudy, live for the most part on brightly colored fruits. The

coloring of rapacious and carrion birds, on the other hand, is always dull and destitute of any decorative hues.

With regard to colors in the external coverings of mammals, Grant Allen[44] says: "The whole series, whether among marsupials, pachyderms, Cetacea, ruminants, Carnivora or Insectivora, show almost uniform tints of black, brown, gray or dingy yellow. It is true that many animals, like the zebras, tigers, spotted deer and giraffes, have very noticeable alterations of light and dark shades, but they do not yield us pure spots of green, blue, red or yellow. When we come to the essentially arboreal mammals, however, the tree rodents and the Quadrumana, we get many comparatively brilliant species. The squirrels are often remarkable for their beautiful colors, and the so-called flying squirrels call for special notice in this respect."

Darwin,[46] in his *Descent of Man,* described the various decorative colorings met with in monkeys. He said: "In very many species the beard, whiskers and crests of hair round the face are of a different color from the rest of the head, and when different are always of a lighter tint, being often pure white, sometimes bright yellow or reddish. The whole face of the South American *Brachyurus calvus* is of a 'glowing scarlet hue'; but this color does not appear until the animal is nearly mature. The naked skin of the face differs wonderfully in color in the various species. It is often brown or flesh-color, with parts perfectly white, and often as black as that of the most sooty negro. In the *Brachyurus* the scarlet tint is brighter than that of the most blushing Caucasian damsel. It is sometimes more distinctly orange than in any Mongolian, and in several species it is blue, passing into violet or gray. In all the species known to Mr. Bartlett, in which the adults of both sexes have strongly-colored faces, the colors are dull or

absent during early youth. This likewise holds good with the mandril and rhesus, in which the face and the posterior parts of the body are brilliantly colored in one sex only."

There is no member of the whole class of mammals which shows such resplendent colors as the adult male mandril; they have been compared with those of the most brilliant birds. The following is the description of one of these animals now in the Zoölogical Society's Gardens: The rather long, harsh hair is dark over the body, but each separate hair is ringed with black and yellow toward the tip, the pattern in certain lights giving a greenish tinge to the fur similar to the shade of other baboons and many other African monkeys. On the forehead there is a crest of hair and on the chin a yellow beard. The naked patches on the buttocks are bright red in the adults. On each side of the face, reaching from the eyes to the nostrils, is a corrugated swelling, divided into a number of longitudinal ridges. These ridges are bright blue and furrows between them purple. The muzzle, of a bright scarlet, is surrounded by a raised border like that of a pig (see Frontispiece).

At first it seems strange that the buttocks should be the part of the body which in some monkeys has acquired the most highly decorative color. In a supplemental note "on sexual selection in relation to monkeys" at the conclusion of his book on *The Descent of Man*, Darwin brings together evidence to show that monkeys so ornamented are proud of their bright red rumps; they turn and display them to old friends and new acquaintances as a form of greeting. These naked parts become more turgid and of a brighter color during the season of love; their display before the female probably acts as a sexual excitement and their proximity to the sexual organs may in this way be explained.

From the foregoing it will be seen that in mammals as

in birds there is a very close correlation between the character of their food and their external coloring. It is only those who have adopted a frugivorous diet that have acquired brilliant hues. How important a good sense of color must be to a fruit-eating animal became clearly demonstrated to me while I was on a visit to Norway; the wild strawberries were then ripe, and several of my party began to gather them; one man, however, could not find any, and it was afterward discovered that he was red-green blind. Had he had to depend for his sustenance on such small fruits, which he gathered for himself, he must soon have perished.

In both birds and mammals bright coloring is often sex-limited, and most frequently it is the male which is the more resplendent. Physiologists are generally agreed that such secondary sexual characters are dependent on internal secretions of the genital organs—testes or ovaries. This point lends considerable support to the Darwinian hypothesis of sexual selection. It is an hypothesis which, if accepted, recognizes the presence of the color-sense in those animals which have acquired sex-limited decorative hues. The theory of sexual selection raised so much controversial discussion that it will be well here to quote what such an authority as Prof. Weissman[47] wrote concerning it fifty years after the publication of *The Origin of Species:* "I really see no reason why we should doubt the power of sexual selection, and I myself stand wholly on Darwin's side. Even though we certainly cannot assume that the females exercise a conscious choice of the handsomest mate and deliberate like the judges in a court of justice over the perfections of their wooers, we have no reason to doubt that distinctive forms (decorative feathers) and colors have a particularly exciting effect upon the female, just as certain odors have among animals of so many different groups, including the butter-

flies. The doubts which existed for a considerable time, as a result of fallacious experiments, as to whether the colors of flowers really had any influence in attracting butterflies, have now been set at rest through a series of more careful investigations. We now know that the colors of flowers are there on account of butterflies, as Sprengel first showed, and that the blossoms of phanerogams are selected in relation to them, as Darwin pointed out. Certainly it is not possible to bring forward any convincing proof of the origin of decorative colors through sexual selection, but there are many weighty arguments in favor of it, and therefore a body of presumptive evidence so strong that it almost amounts to certainty."

At the conclusion of his book, Grant Allen[44] summarizes the whole evolution of color-sense in the following glowing passage: "Insects produce flowers. Flowers produce the color-sense in insects. The color-sense produces a taste for color. The taste for color produces butterflies and brilliant beetles. Birds and mammals produce fruits. Fruits produce a taste for color in birds and mammals. The taste for color produces the external hues of humming-birds, parrots and monkeys. Man's frugivorous ancestry produces in him a similar taste, and that taste produces the various final results of human chromatic art.

"What a splendid and a noble prospect for humanity in its future evolution may we not find in this thought, that from the coarse animal pleasure of beholding food, mankind has already developed through delicate gradations our modern disinterested love for the glories of sunset and the melting shades of ocean, for the gorgeous pageantry of summer flowers, and the dying beauty of autumn leaves, for the exquisite harmony which reposes on the canvas of Titian, and the golden haze which glimmers over the dreamy

visions of Turner! If man, base as he yet is, can nevertheless rise today in his highest moments so far above his sensuous self, what may he not hope to achieve hereafter, under the hallowing influence of those chaster and purer aspirations which are welling up within him even now toward the perfect day!"

It would be interesting to be able to correlate with these views on the evolution of color-sense definite changes in the structure of the retina. Such knowledge as we at present possess permits of this being done in only a tentative manner. The color-sense in man, like the form-sense, is most acute at the macula, where cones only are present. Though the final appreciation of both form and color is evidently a psychological process, it seems to be an essential preliminary step in such appreciation for some change to take place in the end-organs of the nerve fibers in the retina. That the change which gives rise to the sensation of form is essentially different from that which gives rise to the sensation of color is shown by the fact that the one may be deficient without the other being impaired. In cases of congenital amblyopia the form-sense is defective while the color-sense is normal, and in the case of congenital dichromats the color-vision is defective while the form-sense is normal.

The essential factor in the perception of color must be due to some at present unknown reaction, which waves of light of varying wave-lengths produce in the individual cones. As the perception of hues is more acute at the macula than elsewhere, we may infer that the cones in that situation are more capable of undergoing this unknown reaction than those situated in the more peripheral parts of the retina. A comparison of the microscopical appearances of the cones at the macula with those at the periphery

of the retina shows very striking differences in them, both as regards shape and size. The foveal cones, especially those in the very center, are long and slender. The extra-foveal cones decrease in length gradually as they extend toward the periphery, the change being most marked in the outer segment, which also gradually becomes wider.

Careful histological examination of the cones in the retina of congenitally color-blind persons might, I suggest, add considerably to our knowledge of color perception. I have been for some years on the lookout for a specimen in which to make such an examination, but so far have not been successful in obtaining it.

For the perception of colors in the peripheral parts of the field a larger object, intenser light and greater saturation of color is required than in the center. Given cones with a hue-perceiving capacity, these requirements might be largely accounted for by varying degrees of concentration of the cones in different parts of the retina. The retinæ of Primates differ from those of lower mammals in having an area, the macula, in which only cones, closely packed together, are present; we should, therefore, expect that the hue-perceiving faculty of Primates would be endowed with a capacity of seeing small patches of color, color less brilliantly illuminated, and less saturated, than in those mammals in which the cones are more widely scattered. To put it in another way, we should expect that the color-sense of mammals, with widely diffused cones, would be comparable to that of the peripheral portions of the retina of Primates.

The perception of small colored objects is essential for the existence of arboreal animals which live mainly on fruits that they pick up with their fingers. It is by no means essential for the existence of carnivorous or herbivorous mammals. For the former even the capacity of

perceiving color in large masses can have but little use, though in the latter the power of seeing green in large areas might be of some assistance in their search for food. There can be no doubt that bulls in bull-fights are excited into a state of rage by the banderilleros flaunting red cloaks in front of them. I would suggest that the perception of red, presented in this way, excites in them the same instinctive feelings and reactions as that produced by the sight of flowing blood—the inevitable accompaniment of combats in which the flesh is gored with horns. We ourselves use the expression "seeing red" to describe the feelings which excite us to uncontrollable vengeance.

CHAPTER VI.

THE PROTECTIVE MECHANISMS OF THE EYEBALL.

For the development of the conjunctiva it seems essential that the membrane should for a time be converted into a closed sac by the union of the margins of the eyelids together in front of the eyeball. In mammals, like the ruminants, who have to fend for themselves and run beside their mothers directly they are born, the lid margins become separated before birth, so that they are born into the world with their eyes open. The young of nearly all the Carnivora, of most rodents and Insectivora, who spend the first weeks of life in some prepared lair or nest, are born blind, due to the eyelids being still united in front of the eyes. The same applies to the marsupials, whose young for some time after birth are carried about in the maternal pouch. The young of arboreal mammals, such as the lemurs, monkeys and the higher apes, travel about with their mothers from bough to bough directly after birth. The baby monkeys are often carried by their mothers, while the baby lemurs cling tightly to their ventral fur. When born into such an environment it is obviously desirable to be endowed with sight, and we find that these arboreal mammals, like the ruminants, enter the world with their eyes open. Newborn children are in many ways quite as helpless as the newborn Carnivora, but, unlike them, the epithelial union of the margins of their eyelids breaks through before birth; this is doubtless an inheritance from their arboreal ancestors.

All terrestrial mammals, with the exception of man and monkeys, possess three eyelids for the protection of the surface of the eye. Man and monkeys have two, the third eyelid being reduced to a vestigial structure, the semilunar fold.

In birds the third eyelid, or nictitating membrane, is met with in the most highly developed condition; it has in them a muscle directly attached to it which draws it forward in front of the eyeball. In the Mammifera the movements of the third eyelid are most extensive in the Ungulata, and are produced indirectly by the contraction of a muscle which draws backward the eyeball and pushes forward the orbital fat. The third eyelid in mammals is composed of a plate of cartilage covered on both surfaces by mucous membrane. Anteriorly it has a free even margin fitting accurately the surface of the cornea, over which it glides. Posteriorly it terminates in a considerably thickened edge which penetrates into the depths of the orbit on the inner surface of the globe, where it is continuous with a mass of fat. The muscle which draws back the eyeball—the retractor bulbi—arises from the bones at the apex of the orbit, and is inserted into the sclerotic inside the attachments of the recti muscles, between them and the optic nerve. It encircles the latter in a cave-like fashion, hence it is often spoken of as "the choanoid muscle" (Fig. 22). When the eyeball is drawn back in the orbit by this muscle the fat of the orbit, with the base of the third eyelid attached to it, is pressed forward, so that the anterior margin of the eyelid becomes swept across the front of the eye.

In mammals which possess this choanoid muscle the bony outer wall of the orbit is incomplete, the space between the bones being filled up by a fibrous membrane termed the "cornet," which contains muscular tissue, "the orbital

FIG. 22.—Eye of an antelope showing the retractor bulbi or choanoid muscle (*C*). *S*, sheath of Tenon's capsule external to choanoid. *R*, external rectus. *O*, superior oblique. *T*, Tenon's capsule.

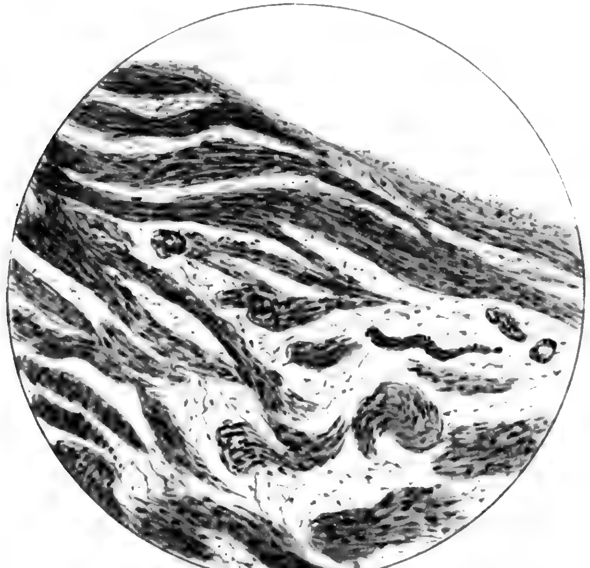

FIG. 23.—Section through Gegenbauer's muscle from the inner surface of the cornea of a sheep.

muscle of Gegenbauer" (Fig. 23). In the Primates, who have no third eyelid or choanoid muscle, there is an outer bony wall to the orbit, the only gap in its continuity being the sphenomaxillary fissure.

The retraction of the eyeball by the choanoid muscle causes the contents of the orbit to become pressed against the fibro-muscular membrane, filling in its outer wall. It is partly the elastic recoil of this membrane, and partly the contraction of Gegenbauer's muscle, which restores the eyeball to its usual position, and brings about the retraction of the third eyelid.

In association with the third eyelid there is a special gland, "the Harderian gland," whose duct opens on its inner surface, and whose secretion is emptied when the eyelid is pressed forward, forming a lubricating fluid for the surface of the cornea. Among mammals this gland is largest in the Ungulata, whose third eyelid is most mobile, smaller in the Carnivora, and absent altogether in monkeys and man who have no third eyelid.

Some mammals possess both a lacrimal gland and a Harderian gland; where, however, the latter is large and the third eyelid is efficient the former is usually small. In monkeys and man, who have no third eyelid or Harderian gland, the lacrimal gland is larger than in other mammals, and largest of all in man.

The functions of the third eyelid are obvious from its anatomical arrangements, it protects the front of the eye from injurious influences, lubricates its surface, and removes any foreign substance which may become lodged on it. In animals, such as the Herbivora, who when feeding hold their heads close to the ground, and in the Carnivora, who do the same in tracking their prey by scent, the presence of such a protective mechanism is of the greatest service

in guarding the cornea from coming in contact with foreign substances, or in their removal should they gain access to the eye.

The grasping of the food in the first place with the hands and the conveyance of it by them to the mouth, as is done by animals who have adopted arboreal life, saves the eyes from much of the risk to which they are exposed when, as in grazing, the food is seized directly with the mouth. The development of the forelimbs into organs of delicate tactile sensibility, capable of picking up minute particles, has made it possible for them to be used for the removal of foreign bodies from the eye, and thus, as suggested by Le Coq, to play the part of the third eyelid in a way which is not possible for hoofs or claws.

The greater flow of lacrimal secretion in response to the irritation of foreign bodies supplies also an hydraulic apparatus for removal of foreign bodies, to replace the mechanical arrangement of the third eyelid.

Not only as the third eyelid becomes a superfluous structure in Primates, but the retraction of the eye which its use entails would be a source of trouble and inconvenience to them. The movement of the eyes backward and forward in the orbit in animals who have assumed the erect or semierect posture would considerably interfere with the accuracy of stereoscopic vision and of accommodation and convergence.

The vestigial remains of the third eyelid persist in man and monkeys as the semilunar fold. Owen[48] says that a remnant of the choanoid muscle is to be found in the lower Quadrumana, in the form of a few fibers detached from the inner part of the recti to be inserted into the sclerotic nearer the entry of the optic nerve. Sir John Bland-Sutton[49] has recently suggested that Tenon's capsule is really the representative of this muscle in man. He says: "A critical

examination of Tenon's capsule in the orbit of man and monkeys convinces me that it is the degenerated representative of the retractor bulbi as surely as the little pleat of mucous membrane, known as the semilunar fold, is the vestige or remnant of the third eyelid."

Motais[50] has found the capsule of Tenon constructed in a uniform manner in all classes of vertebrates; it presents, he says, only slight variations due to differences in the arrangements of the ocular muscles. He has published pictures showing its arrangements in the eyes of a horse and of a cow, in which also the choanoid muscle is present. I have found it present myself in dissections I have made of an antelope (Fig. 22) and of a sheep. It ensheaths, and stretches between, the recti muscles, and forms, moreover, a sheath to the choanoid muscle itself. Inasmuch, then, as Tenon's capsule is found in animals in whom the choanoid muscle is present, it would seem impossible to regard it as a vestigial remnant of the muscle when absent.

Lindsay Johnson[3] states that he met with a case of an obvious membrana nictitans in a youth which was capable of slight movement and extended in a crescent form nearly as far as the cornea. He does not say, however, whether this movement of the membrane was effected by any accompanying displacement of the eyeball backward. In 1912, S. E. Whitwall[51] recorded an instance of a retractor bulbi muscle present in both orbits of a man, aged fifty years. He states that vestiges of it are also met with in some monkeys (*e. g.*, Macacus rhesus).

Though the evidence of any vestigial remains of the choanoid, or retractor bulbi muscle, is very doubtful, the presence of vestigial remains of Gegenbauer's orbital muscle, or, as I suggest it might be well termed, "the protrusio bulbi muscle," is clear and conclusive.

H. Müller[52] in 1858 first described how he had found flat muscle fibers in the inferior orbital fissure in man, corresponding to that met with in the orbital membrane of Mammalia. He also described how it was the antagonistic contraction of this membrane, by muscular action, which restored the eyeball to its position in the socket after it had been drawn back by the retractor. The muscle he found was composed of unstriated fibers, and was stimulated into action by irritation of the cervical sympathetic nerve.

Sir William Turner[53] in 1862 wrote an article entitled "Upon a Nonstriped Muscle Connected with the Orbital Periosteum of Man and Mammals." In it he says: "While engaged in making a dissection in the human subject during the winter session of last year, of the inferior maxillary, or second division of the fifth cranial nerve, my attention was attracted to a pale reddish, soft mass, filling up the narrow chink of the sphenomaxillary fissure, and extending from the sphenoid fissure in the sphenoid bone to the infraorbital canal in the superior maxillary bone. It was evidently connected to the superior (ocular) aspect of the periosteum of the orbit, and it was pierced by the orbital branch of the superior maxillary nerve. Since the period of making the above observation I have availed myself of several opportunities of examining the same region in other subjects, and have constantly observed appearances of a nature similar to that just described. The amount of the reddish mass and the depth of its tint varied slightly in different instances. Frequently it was so pale as scarcely to attract attention, which may perhaps be the reason why it has so long been neglected by anatomists. When carefully examined with the naked eye, or still better with a single lens, it was seen to exhibit a fibrous appearance."

The existence of these unstriated-muscle fibers in man,

which may be regarded as the analogue of the "protrusio bulbi muscle" in lower animals, and which is supplied by the cervical sympathetic nerve, is of considerable clinical interest.

First, because it has been noted that slight protrusion of the eyeball, or exophthalmos, may occur from stimulation of the cervical sympathetic, and slight recession or enophthalmos from its paralysis. Secondly, because overaction of this muscle offers the most satisfactory explanation of the exophthalmos which occurs in connection with Graves' disease. As stated by André Crotti[54] the exophthalmos in this affection generally develops slowly, but may come on rapidly. It is liable to fluctuations varying with the physical and mental condition of the patient. It may subside entirely after operation, on the same day as the operation, to reappear again a few days later. It also disappears after death. All these circumstances are consistent with the contraction or relaxation of a muscle which has the power of pushing forward the globe. The amount of protrusion which its contraction produces would naturally vary with the state of its development; like other muscles it would tend to hypertrophy and increase in power by prolonged stimulation. By such increase in its power the increase in the amount of the exophthalmos might be accounted for in the cases of long standing.

Another symptom of the disease, viz., retraction of the upper lid, is due to contraction of muscle fibers supplied by the cervical sympathetic nerve. This muscle, which was also first described by Müller, is also named after him, and, like the muscle about the sphenomaxillary fissure, is composed of unstriated fibers.

A number of other theories have been suggested to account for the exophthalmos in this disease, which may be summarized as follows:

(*a*) Abnormal deposit of retrobulbar fat.

(*b*) Relaxation of recti muscles from fatty degeneration.

(*c*) Serous infiltration of the retrobulbar connective and fatty tissue of the orbit from vasomotor disturbance caused by toxemia from thyroid disturbance.

(*d*) Venous congestion.

(*e*) Localized arterial dilation.

Postmortem examinations have failed to substantiate the presence of any of these conditions. Localized arterial dilation would produce pulsating exophthalmos. Venous orbital congestion would, if it produced proptosis, also produce retinal venous dilation—a condition which is never seen. None of these theories will account for the fluctuations in the degree of the proptosis in the way in which contraction and relaxation of a muscle tissue will do.

The effect of the contraction of Müller's muscle in the human eye, situated as it is in the loose periosteum of the orbit, would be, as in other animals, to press forward the fat of the orbit and consequently the eyeball which lies in front of the fat. Under such circumstances, if, in a case of exophthalmos, an incision was made through the orbitotarsal ligament, we should expect the fat, being pushed forward and kept in a state of tension, to well up through the incision. We should also expect that in extreme cases of exophthalmos, in which ulceration of the cornea was threatened, recession of the eye and beneficial results might attend removal of some of the fat. Foster Moore[55] has recently recorded how he performed an operation of this description, removing a "heaped-up tablespoon of fat" through an incision which extended the whole length of the lower conjunctival fornix. Afterward the lids were easily approximated and sewed together over the front of the eye, so that the eye was preserved. From the result

produced in this case he infers, as I think wrongly, that the proptosis must have been due to an excess of fat. The circumstances of the case may equally well be accounted for by a protrusion forward of orbital fat due to muscular contraction.

Though the vestigial character of the plica semilunaris is well recognized, the vestigial character of the caruncle seems to have been overlooked. A study of the morphology of the parts about the inner canthus of the eye in mammals shows variations of a marked character, not only in the different natural orders, but also in the different species. In kangaroos the inner canthus is prolonged into a triangular flat area, kept moist by the overflow of tears; it is continuous with the skin of the nose and is fringed with fur. A somewhat similar bald area, fringed with fur, is met with in the Carnivora, varying, however, in size and shape in different species. It is among the Ungulata that the most conspicuous developments are met with in this region, more especially among the ruminants (Fig. 24). In them the inner canthus is prolonged for a considerable distance inward and downward, sometimes as a thin streak and sometimes as a broad band. The band or streak ends usually in an inverted fold, for the lodgment of which there is, in some animals, a depression in the lacrimal bone. This fold or recess is termed the "suborbital pit," and by French naturalists, as it is kept moist by lacrimal secretion, "larmier." The whole of the integumentary area leading from the eye to the recess and the recess itself is composed of numerous sebaceous glands opening into dwarfed hair-follicles (Fig. 25); at the bottom of the recess a few short hairs are frequently seen projecting from among the glands. Around this glandular structure are bands of muscle fibers, which by their contraction bring about a protrusion of the

secreting surface. The secretion from the glands has a strong musky odor, and these suborbital pits reach their greatest size in animals which possess an acute sense of smell; especially is this so in animals such as deer and

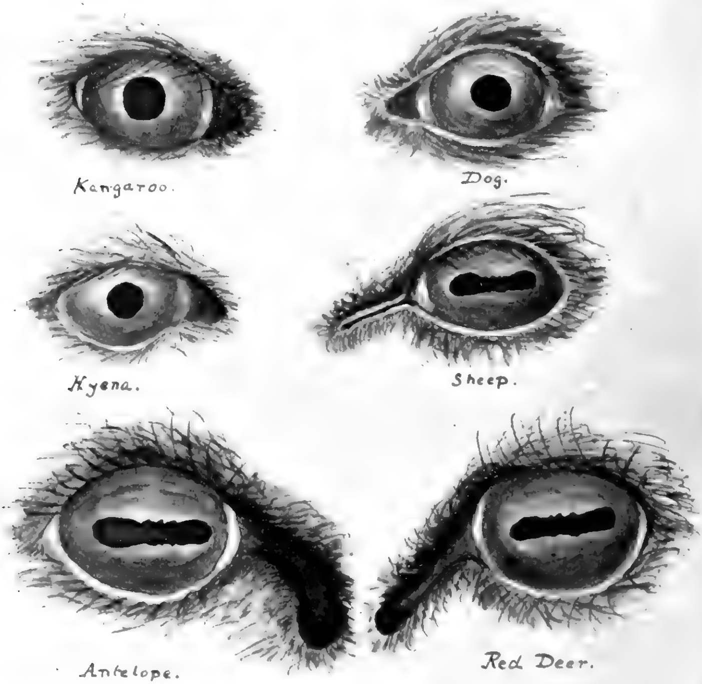

Fig. 24.—Showing the arrangement of parts at the inner canthus in different mammals.

antelopes, in whom smell is what may be termed a "distance-sense," in contradistinction to a contact-sense, such as it is in most of the Carnivora. These odoriferous glandular organs probably form a means by which a stray member

of a herd may be guided to rejoin its fellows. They seem also to have some connection with the sexual function, as they are usually larger in the male than in the female, and their growth is said to be arrested by castration. In arboreal

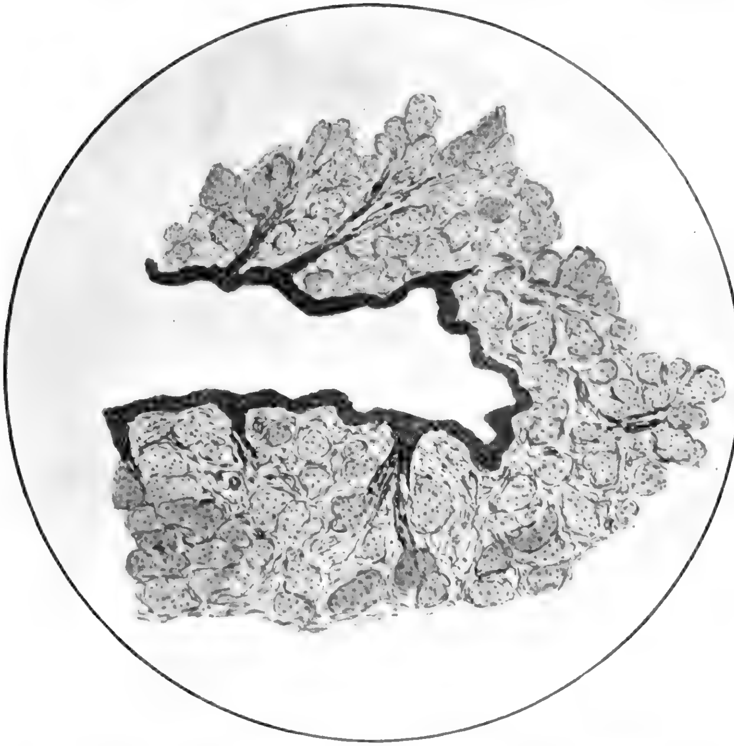

Fig. 25.—Lining membrane of the suborbital pit of a sheep.

mammals, like monkeys and anthropoid apes, the sense of smell is of but little use; the olfactory organs are comparatively poorly developed, and the odoriferous organs at the inner angles of eyes have dwindled into vestigial

structures. The caruncle, both in man and monkeys, has become contracted up into a small elevation cut off from any continuity with the skin of the face by the margins of the eyelids, which have completely closed round it, so that it is entirely located in the lacrimal bay. That it really is a vestige of the secreting odoriferous areas met with in other mammals seems evident from its containing remnants of all the constituents of such areas. The following is the description of the structure of the caruncle given in Quain's *Anatomy:* "Occupying the recess of the angle at the border of the plica semilunaris is a spongy-looking reddish elevation (caruncula lacrimalis), formed by a small insulated portion of skin containing a few large, modified sweat-glands, also a group of sebaceous glands which open into the follicles of very fine hairs. There is further found in it a small amount of plain muscular tissue (H. Müller) as well as a few cross-striated muscular fibers." It is also stated that in man, as in some animals, the caruncula lacrimalis retains its connection with the skin at the inner canthus. It is interesting to note in connection with this matter, that the reduction of what must have been a large suborbital pit to a comparatively small bald area at the inner canthus, can be traced in the evolution of the horse. In the skull of the modern horse no depression is found in the lacrimal bone in front of the orbit for such a glandular structure. In the fossil remains of the skulls, from the Pliocene epoch, of the *E. sivalensis* of India and of the *E. stenois* of Europe, traces of the depression or gland-cavity are met with, while in the fossil skulls of the Hipparion, a three-toed horse from Miocene beds, there is a very large depression in the bone in front of the eye.

In conclusion, I would claim that the changes in the visual organs of mammals, produced by the adoption of

arboreal life, increased both the range and accuracy of their powers of observation for natural phenomena. It was in this way that the portal became opened for the evolution of the mental faculties of memory and inference—faculties which enabled man's anthropoid ancestors, on descent from the trees, to subdue their foes, to become successful hunters and to adopt an omnivorous diet. It would seem, therefore, that some such study of the visual organs as I have attempted in this lecture is necessary for fully understanding the way in which man gained his predominant position in the animal kingdom.

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